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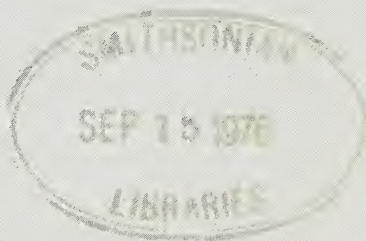
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LATE PLEISTOCENE MOLLUSCAN FAUNAS FROM UPPER TERRACES
OF THE PALOS VERDES HILLS, CALIFORNIA

By LOUIE MARINCOVICH

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LATE PLEISTOCENE MOLLUSCAN FAUNAS FROM UPPER TERRACES OF THE PALOS VERDES HILLS, CALIFORNIA¹

By LOUIE MARINCOVICH²

ABSTRACT: The Palos Verdes Hills of southern California bear a sequence of thirteen Pleistocene marine terraces that locally contain abundant molluscan remains. Study of faunas from several upper terraces—five, seven, nine, and twelve—shows them to have essentially the same character as the better-known lower terraces (terrace levels one to four). The entire terrace sequence at the Palos Verdes Hills is considered to be of late Pleistocene age. The mollusks are inferred to have lived mainly in rocky shore habitats in water depths no greater than about 30 metres, and in a marine hydroclimate cooler than the one along the modern Palos Verdes coastline. The large number of southern rocky shore species required a local site of warmer water or the periodic introduction of southern species by warm counter-currents. Forty-seven species of mollusks found in the Pleistocene deposits of the Palos Verdes Hills were not previously reported.

INTRODUCTION

The Palos Verdes Hills, near Los Angeles, California (Fig. 1), bear a sequence of 13 emergent Pleistocene marine terraces that locally contain abundant molluscan faunas. Study of these terrace deposits by Woodring, Bramlette, and Kew (1946) established their general age and nature, but was based mainly on deposits of the four lowest terraces (here referred to collectively as the lower terraces). Although these workers considered all of the terraces to be of late Pleistocene age, others believed that the upper terraces could be of early Pleistocene or even late Pliocene age (Bandy, *in* Bandy and others 1964; Wahrhaftig and Birman 1965). In addition to uncertainties about age, there was relatively little information on the paleoecology of the upper terrace faunas, owing to insufficient collecting. For example, the southern rocky shore faunal element common on the lower terraces had never been found above the fifth terrace level, and its presence on higher terraces would influence interpretations of regional marine hydroclimate during the Pleistocene. Most of the upper terraces (terrace levels five to thirteen) apparently had never been searched for the extinct rocky shore molluscan assemblage, characterized by the gastropod *Calicantharus fortis* (Carpenter), commonly found in higher terrace deposits of the southern California islands. The presence of this faunal element in the higher terraces of the Palos Verdes Hills would provide a possible first means of correlation with the higher terraces of the islands.

¹REVIEW COMMITTEE FOR THIS CONTRIBUTION:

WARREN O. ADDICOTT
JAMES W. VALENTINE
EDWARD C. WILSON

²Research Associate in Invertebrate Paleontology, Natural History Museum of Los Angeles County, and U.S. Geological Survey, 345 Middlefield Rd., Menlo Park, California 94025.

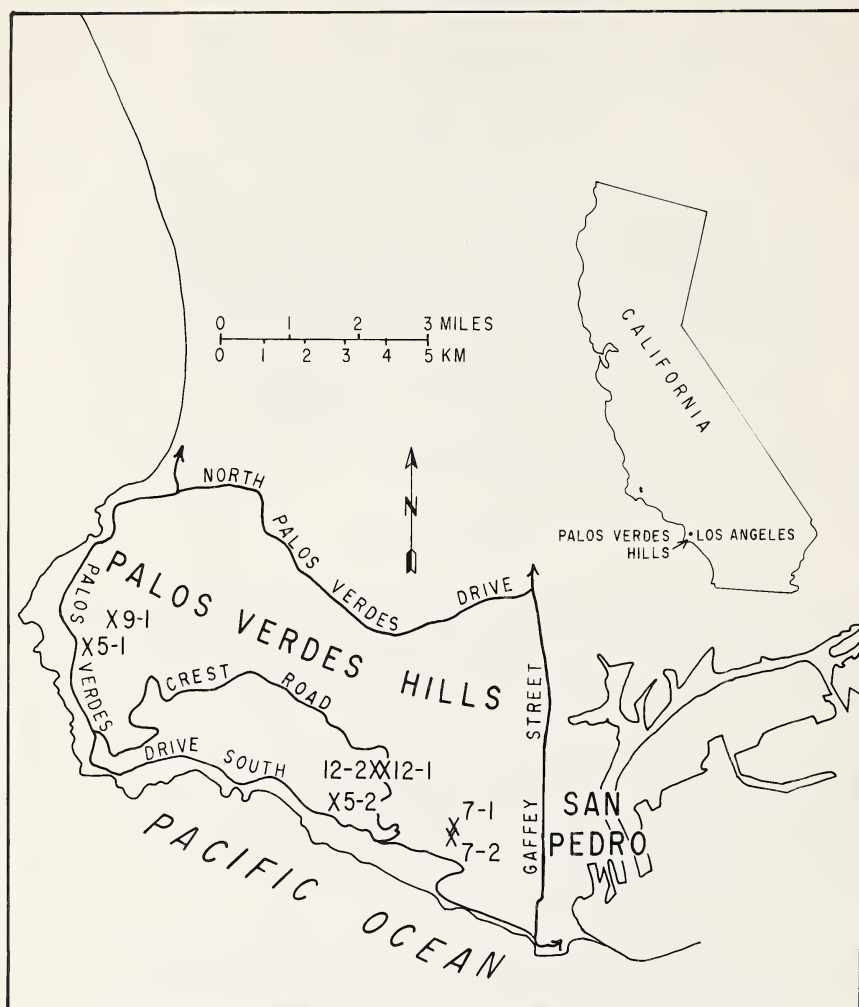


FIGURE 1. Index map of Palos Verdes Hills, showing Pleistocene fossil localities. First part of each locality number indicates terrace level on which locality is situated.

Search of the Palos Verdes Hills for all exposures of Pleistocene marine deposits above the fourth terrace level resulted in seven collections from terrace levels five, seven, nine, and twelve. Only one of these localities, locality 12-1, had been found by earlier workers (Woodring and others 1946); the new exposures presumably were not available to Woodring and earlier workers because few artificial cuts existed on the higher terraces prior to World War II. Part of the fossil material in these collections was made available by William H. Easton, University of Southern California. All specimens have been deposited in the Invertebrate Paleontology

Section, Natural History Museum of Los Angeles County. James H. McLean of the Museum aided in the identification of several species and made available his unpublished notes on Pacific Coast mollusks. Spencer Thorpe, El Cerrito, California, identified the chiton remains. I thank Warren O. Addicott and John G. Vedder, U.S. Geological Survey, and James W. Valentine, University of California at Davis, for making helpful comments on this study.

LATE PLEISTOCENE MOLLUSCAN FAUNAS

PREVIOUS STUDIES

The geology and paleontology of the Palos Verdes Hills has attracted many workers, beginning with Trask (1855), who gave a brief general description of the rock types in the San Pedro area and mentioned the presence of fossil marine mollusks "upon the summits of the cliffs among the fine alluvium and soil," probably the earliest reference to Pleistocene terrace deposits of this area. This work was followed by numerous others, many of which included descriptions and discussions of the Pleistocene mollusks in and around San Pedro. These works and many others dealing only indirectly with the Pleistocene deposits are listed chronologically by Woodring and others (1946). Kennedy (1975) brought this compilation up to date, annotated it, and included it in a review of paleontologic records of this area.

Gabb (1869) gave the earliest large list of Pleistocene fossils from the San Pedro area, including 86 species of mollusks, but did not specify the localities from which the fossils had come; it was left for Arnold (1903) to describe the formations comprehensively. His monographic work on the San Pedro Pleistocene strata listed nearly 400 species of mollusks, many of them new, and stimulated further work on these deposits. Numerous systematic papers and reports on new finds of early and late Pleistocene molluscan assemblages followed Arnold's work. Grant and Gale (1931) included records of Pleistocene mollusks from the Palos Verdes Hills in their monumental catalog, but speculated only incidentally on paleoecology. With the exception of Berry's (1922) treatment of the chitons, the next comprehensive work was the areal report on the Palos Verdes Hills by Woodring and others (1946). Their report, the most complete account to date of the geology and paleontology of the Palos Verdes Hills, describes with varying completeness the fossil assemblages from 142 localities, of which 114 were in Pleistocene deposits. The detailed composition of the molluscan faunas in the lower and upper Pleistocene formations is presented in this work, along with a discussion of the environments represented by the faunas. The presentation is most complete for the lower Pleistocene units and for the marine deposits on the lowest emergent terrace. The molluscan faunas of the upper terraces were only generally outlined, probably owing to a paucity of well-preserved material, and the only complete faunal list was for a single locality on the twelfth terrace. Kennedy (1975) discussed Pleistocene faunas of the San Pedro area but presented no new faunal lists from Palos Verdes Hills Pleistocene localities.

The most recent papers on the upper terrace deposits are Valentine's (1961, 1962) interpretations of some paleoecological aspects of the molluscan faunas neglected

by earlier workers and a note on the present study by Marincovich (1971). The earlier of Valentine's papers deals briefly with the upper terraces; the more recent paper is concerned mainly with terrace levels four, five, and six.

STRATIGRAPHY

The greater part of the Palos Verdes Hills is made up of moderately deformed middle and upper Miocene marine sedimentary rocks, at least 1,200 metres thick, consisting of mudstone and diatomaceous, cherty and phosphatic shales that form part of the Monterey Formation. Relatively rare molluscan and fish remains are known from these strata (Woodring and others 1946). Microfossils indicate deposition in bathyal and abyssal depths (Ingle 1967).

Lower Pliocene deposits of the Fernando Formation consist of as much as 45 metres of soft, bluish-gray siltstone in the Hills, but thicken northward to as much as 1,500 metres in the Los Angeles Basin. Foraminiferal and molluscan evidence (Woodring and others 1946; Ingle 1967) suggests deposition at bathyal or abyssal depths. The deposits crop out discontinuously along the northern flank of the Palos Verdes Hills, where they rest disconformably upon Miocene rocks. These deposits lie disconformably below lower Pleistocene deposits and are truncated in places by upper Pleistocene terrace deposits.

The lower Pleistocene rocks consist of marine sandstone, siltstone and marl present along the eastern and northern margins of the hills. These deposits form the San Pedro Formation, which is divided into three members (Poland and Piper 1956), in ascending order: the Lomita Marl Member, Timms Point Silt Member, and an unnamed sand member. The unnamed sand member has been referred to by some workers (Woodring and others 1946; Valentine 1961) as the San Pedro Sand, but this name would conflict with the formational name according to the Code of Stratigraphic Nomenclature. The maximum thickness of the San Pedro Formation in outcrop is not over 105 metres; the maximum subsurface thickness is thought to be about 180 metres (Woodring and others 1946). The three members intergrade or are unconformable wherever their contacts are exposed, and the lowest part of the Lomita is thought to be slightly older than the rest of the San Pedro Formation. Molluscan faunal trends suggest shoaling upsection within sublittoral depths for the Lomita and the unnamed sand member (Valentine 1961). Outer sublittoral mollusks from these strata may have been reworked into the upper Pleistocene beds during terrace cutting.

Upper Pleistocene marine strata in the Palos Verdes Hills are preserved on remnants of the 13 recognized major terraces (numbered 1 to 13 in ascending order by Woodring and others 1946). The shoreline angle of the highest terrace is at an elevation of 356 metres, the lowest at 2 metres. Possibly four to six submarine terrace levels of late Pleistocene age lie adjacent to the southern and west coasts of the Palos Verdes Peninsula to depths of about 90 metres (Emery 1958, 1960). The marine terrace deposits of the Palos Verdes Hills constitute the Palos Verdes Sand (Marincovich 1970; Kennedy 1975), which ranges from fine silty sand to coarse-grained sand and gravel up to about 5 metres thick that locally contains abun-

dant and well-preserved molluscan remains. Fossil assemblages from the lowest terrace contain a few northern and many southern extra-limital mollusk species (Woodring and others 1946; Valentine 1961). This distinctive array of molluscan communities has lent itself to the naming of the late Pleistocene Verdean faunal province by Valentine (1961).

Deposits on the Pleistocene marine terraces vary in thickness from nearly 5 metres at the seaward edges of the terraces to a few centimetres at the landward edges. However, marine sediments do not always occur on each terrace level, and marine deposits more than 1 to 1.5 metres thick are the exception. Although Woodring and others (1946) list 67 Pleistocene fossil localities on the terraces, the deposits are discontinuous, generally occurring as laterally restricted pods or lenses and not as extensive beds. This spotty occurrence of fossiliferous sediments is due in part to the concealment by the extensive nonmarine cover, but possibly also to primary deposition in slight depressions or pockets worn into the Miocene platform surface. As Addicott (1966) has pointed out, this could possibly protect such deposits from further reworking and help insure their preservation.

FAUNAL COMPOSITION

The Pleistocene terrace fauna of the Palos Verdes Hills includes at least 700 species of larger invertebrates. Mollusks are the dominant faunal element, followed in order of species abundance by foraminifers, bryozoans, echinoids, barnacles, and corals. Arnold (1903) recorded nearly 400 molluscan species from the lowest terrace at San Pedro, and subsequent workers listed 348 additional mollusks from the terrace above the lowest one (including species in this report). One hundred and seventy-four molluscan species were identified for this report (Table 6), including 47 taxa not previously recorded from marine terraces of the Palos Verdes Hills (Table 1). A detailed survey of the non-molluscan terrace fossils has never been made.

The presence of *Collisella edmitchelli* (Lipps) on terraces seven and twelve marks the first occurrence of this species on the mainland, as it had been found only on San Nicolas Island at localities ranging in elevation from less than 120 metres to more than 240 metres (Lipps 1963). Although Lipps considered *C. edmitchelli* to be most closely related to *C. limatula* (Carpenter) on the basis of shell sculpture, *C. edmitchelli* in the present collections intergrades completely with specimens of *C. scabra* (Gould), one of the most widespread limpets in Pleistocene terrace deposits throughout southern California. The sculptural features of *C. limatula* and *C. edmitchelli* do not intergrade in specimens from the Palos Verdes Hills, contrary to findings for San Nicolas Island Pleistocene specimens (Lipps 1963).

The minute bivalves *Lasaea cistula* Keen and *Lasaea subviridus* Dall intergrade in the present collections, a condition noted by Valentine (1962) for these species at a locality on terrace five. It is impossible to separate the species of *Cerithiopsis*, of which there are undoubtedly several, because their worn condition does not permit examination of sculptural features.

TABLE 1

Pleistocene mollusks not previously reported from terraces (terrace levels 1 to 13) in the Palos Verdes Hills.

BIVALVES

Milneria cf. *M. minima* Dall
Nettastomella rostrata (Valenciennes)
Parapholas cf. *P. californica* Conrad
Pristes oblonga (Carpenter)
Saxidomus nuttalli Conrad
Semele incongrua Carpenter
Semele rupicola Dall
Ventricolaria fordi (Yates)

GASTROPODS

Acteocina culcitella (Gould)
Acteocina cf. *A. harpa* (Dall)
Alvinia aequisculpta Keep
Alvinia cosmia (Bartsch)
Balcis cf. *B. thersites* (Carpenter)
Barleeia cf. *B. subtenuis* Carpenter
Bitium purpureum (Carpenter)
Clathromangilia interfossa (Carpenter)
Clathromangilia variegata Carpenter
Collisella edmittchelli (Lipps)
Cymatium sp.
Diodora arnoldi McLean
Haliotis rufescens Swainson
Homalopoma fenestrata (Dall)
Lirularia cf. *L. acuticostata* (Carpenter)
Lirularia succincta (Carpenter)
Lucapinella callomarginata (Carpenter)

Maxwellia gemma (Sowerby)
Megathura crenulata (Sowerby)
Metaxia convexa (Carpenter)
Mitromorpha intermedia Arnold
Odostomia aepynota Dall & Bartsch
Odostomia cf. *O. helga* Dall & Bartsch
Odostomia aff. *O. hemphilli*
 Dall & Bartsch
Odostomia cf. *O. lucca* Dall & Bartsch
Odostomia navisa Dall & Bartsch
Odostomia cf. *O. trachis* Dall & Bartsch
Opatia montereyensis (Dall)
Parviturbo acuticostata (Carpenter)
Petalonchus cf. *P. macrophragma*
 Carpenter
Petalonchus montereyensis Dall
Rissoina dalli Bartsch
Volvarina taeniolata Mörch

CHITONS

Callistochiton decoratus Pilsbry
Lepidochitona keepiana Berry
Mopalia cf. *M. lowei* Pilsbry
Mopalia wosnessenski Middendorff
Nuttallina californica (Reeve) or
N. fluxa (Carpenter)
Stenoplax heathiana Berry or
S. fallax Carpenter

A large and complete specimen of the red abalone, *Haliotis rufescens* Swainson, is reported here for the first time from terraces of the Palos Verdes Hills. Absence of this species in previous collections was probably due to the incompleteness of specimens found, for fragments would most likely be mistaken for the common *Haliotis cracherodii* Leach, the only other abalone known from the terraces.

The addition of seven species of *Odostomia* to the terrace fauna is more indicative of fortuitous preservation than of basic changes in the marine environment. Four of the seven species are from localities 7-2 and 12-2, which appear to have been situated farther offshore than most of the upper terrace localities. *Odostomia* cf. *O. trachis* Dall and Bartsch is of further interest because it is restricted in its known modern range to San Pedro Bay (Dall and Bartsch 1909), while the present record from terrace seven is the first known fossil occurrence of this species. If the Pleistocene and Holocene records are accurate, this species has maintained a very restricted geographic range throughout much of the Pleistocene while profound thermal changes were taking place in the marine hydroclimate.

The occurrence of the minute bivalve *Bernardina bakeri* Dall on terrace seven is only the fourth fossil record of this species (Valentine 1962; Valentine and Lipps 1963; Vedder and Norris 1963), and the equally small bivalve *Pristes oblonga* (Carpenter) on terrace nine has apparently never before been reported as a fossil. The only extinct species in the present collection is *Rissoina pleistocena* Bartsch, known only from upper Pleistocene deposits of southern California.

MODE OF FORMATION

All of the localities visited during this study contain abundant broken and abraded shell debris in a poorly sorted matrix, attesting to some degree of transportation before final deposition. However, localities 12-2, 9-1, 7-2, and 5-2 contain some fairly well-sorted sediments which have well-preserved fossils in them that appear not to have been transported far. Specimens of *Haliotis cracherodii* Leach and *H. rufescens* Swainson from localities 12-1 and 12-2 are commonly unworn and some retain their delicate shell margins intact. Complete specimens of *Astraea undosa* (Wood) and *Cypraea spadicea* Swainson, rarely found in terrace deposits, provide more evidence for lack of post-mortem transport at locality 12-2. The large number of well-preserved minute species at localities 12-2, 9-1, and 7-2 also suggests that there has not been significant post-mortem transport. Broken and abraded specimens are to be expected in deposits representing high-energy marine environments, such as those of the Palos Verdes terraces, but easily destroyed minute specimens may be preserved by lodging in the interstices between larger shell fragments and coarse rock debris. Larger gastropod shells are commonly used as portable shelters by hermit crabs and thereby exposed to a longer period of abrasion than if they were immediately incorporated into the substrate. The most convincing evidence for an undisturbed deposit is at locality 9-1, where large numbers of the bivalve *Epilucina californica* (Conrad) were found with their valves intact. The interiors of the shells are filled with sand, but remnants of the ligaments are preserved in some individuals. Oriented infaunal bivalves such as observed by Addicott (1966) in Pleistocene sediments of central California are compelling evidence for undisturbed deposition, but were not found in the terrace deposits of the Palos Verdes Hills.

Besides possibly being transported and abraded during their addition to the substrate, the terrace fossils could have been reworked by wave action during retreat of the sea (uplift of the land), and later during subaerial formation of the non-marine terrace cover. Retreat of the high-energy breaker zone from its position at highest sea stand on a given terrace level would cause erosion of the previously formed terrace deposits. Depth of effective wave abrasion extends to about 10 metres (Dietz and Menard 1951; Bradley 1958) and length of exposure of the terrace deposits to wave erosion depends on the rate at which the sea retreated from the land. This, in turn, is a resultant of the differential rates of movement of the tectonically unstable Palos Verdes block and a rising or sinking sea level.

At numerous fossil localities in the Palos Verdes Hills worn and broken fragments of a few species are the only molluscan fossils found; these deposits have

undoubtedly been extensively reworked during deposition or afterward. Withdrawal of the sea from the maximum shoreline attained during cutting of a given terrace would have subjected deposits on that terrace platform to a vigorous abrasion (Addicott 1966) and might have similarly affected terrace deposits formed previously at a lower elevation. Destruction of fossils would also occur if sea level again rose enough to erode deposits formed during an earlier cycle of marine inundation.

The preservation of relatively undisturbed fossil deposits on several terraces might indicate rapid retreat of the sea from its points of greatest inundation. As Addicott (1966) has noted, gradual retreat of the high-energy breaker zone probably would destroy all traces of inner sublittoral deposits and possibly admix littoral invertebrates. Since a common inner sublittoral and a small but persistent outer sublittoral molluscan element are present in all of the thoroughly studied Palos Verdes terrace deposits, it is possible that retreat of the Pleistocene seas was a relatively rapid event after cutting of each terrace platform.

Additional abrasion and chemical weathering of the terrace fossils occurs during subaerial formation of the nonmarine terrace cover. Commonly throughout the Palos Verdes Hills, the alluvial cover lies upon the terrace platform cut into Miocene rocks, without intervening Pleistocene deposits. This complete absence of Pleistocene sediments and fossils most probably resulted from formation of the nonmarine terrace cover, as even vigorous erosion by the retreating sea would probably leave some evidence of its former presence. The lack of cobbles and other large debris is still puzzling. Scattered Pleistocene mollusks, usually in poor condition, commonly occur in the nonmarine terrace cover. They were probably derived from two sources: Indian kitchen middens, very common in the Palos Verdes Hills, and marine terrace deposits reworked during formation of the nonmarine alluvium. Once buried in kitchen middens, the shells became scattered throughout the nonmarine deposits by natural processes of erosion, including burrowing animals, and by agricultural, construction, and earthmoving activities. In most cases it is impossible to determine the source of scattered mollusks in the nonmarine terrace cover.

RELATIVE SIZE OF THE UPPER TERRACE FAUNAS

The largest assemblages of Pleistocene mollusks on the west coast of North America are those from Newport Bay, California (Kanakoff and Emerson 1959), and Magdalena Bay, Baja California, Mexico (Jordan 1936), each of which contains more than 400 species of mollusks and numerous other invertebrates. Such large faunas are made up of species representing more than one biotope and are not directly comparable with the Palos Verdes Hills upper terrace faunas, which almost exclusively contain species restricted to rocky open coastlines.

Faunas of the Palos Verdes Hills upper terraces include 348 taxa of mollusks reported in the literature (including those herein), by far the largest assemblage of Pleistocene rocky shore invertebrates along the California coast. The present collection contains 174 species of mollusks, of which 47 are new to the Palos Verdes

Hills terrace deposits (Table 1). Faunas of about 100 to 150 species of mollusks are known from terraces on Anacapa Island (Valentine and Lipps 1963), San Nicolas Island (Vedder and Norris 1963), Santa Barbara Island (Lipps and others 1968), and Point Loma (Valentine and Meade 1961) in southern California. Pleistocene faunas of similar size are recorded from Cayucos (Valentine 1958) and near Santa Cruz (Addicott 1966) in central California, and from Punta China, Baja California (Emerson 1956). Vedder and Norris (1963) report more than 275 taxa from the lowest emergent terrace in the Laguna Beach-Dana Point area of southern California. Valentine (1962) reported 94 molluscan taxa from the fourth terrace of the Palos Verdes Hills, and Woodring and others (1946) reported, but never fully recorded, a collection of 109 species from the second terrace. The largest assemblage from a single terrace in the present collection is 88 species from terrace twelve. Numerous other Pleistocene terrace localities with smaller assemblages of mollusks are known along the coasts of California and Baja California.

The large size of Pleistocene molluscan assemblages facilitates study of their paleoecology. But even these large faunas may not provide an accurate picture of what the ancient faunas were like. Valentine (1967) records 1,222 species of shelled benthic mollusks from the modern Californian molluscan province [as defined by Valentine (1966), and Durham (1967)] notes that the recorded Pleistocene invertebrate fauna of California is only about two-thirds as large as the living preservable fauna of the same region. Because of the original high-energy depositional environment of terrace fossils and the erosion and weathering to which they have been exposed, the faunas of the Palos Verdes upper terraces probably represent less than two-thirds of the original Pleistocene molluscan fauna that inhabited the coastline.

BATHYMETRY

The upper terrace faunas were deposited in depths ranging from the intertidal zone to about 30 metres. Most upper terrace mollusks are restricted to their present bathymetric ranges to the intertidal zone or to inner sublittoral depths (0 to 100 metres; Hedgpeth 1957). Only 11 species in the present collection are restricted exclusively to sublittoral depths (Table 2), and of these only five have the greater part of their ranges in the deeper part of the inner sublittoral zone. The deepest-ranging species in the present collection is *Fusinus arnoldi* (Cossmann), which is known to range from 30 to 216 metres (Burch 1945) but seems to be most common at about 200 metres (J. H. McLean, *oral communication*).

The majority of the species restricted to the inner sublittoral zone (Table 2) have their upper depth limits between 20 and 40 metres, suggesting that most of the sublittoral elements in the terrace faunas came from no shallower. This is considerably below the commonly accepted 10-metre limit of effective wave-produced submarine erosion (Dietz and Menard 1951; Bradley 1958), but is still apparently well within the zone susceptible to active, if irregular, sand transport (D. S. Grosline, *personal communication*). It is thus possible that mollusks in this depth range could have been transported inshore to the sites of the present terrace deposits. The

TABLE 2

Species with exclusively sublittoral bathymetric ranges, showing their occurrence at upper terrace localities and modern habitat data. F = fragment

	TERRACE LOCALITIES							HABITAT (Burch 1945, 1946)
	5-1	5-2	7-1	7-2	9-1	12-1	12-2	
BIVALVES								
<i>Semele incongrua</i> Carpenter	...	...	...	...	1F	...	...	30-5m, nestling or in sand
<i>Ventricolaria fordii</i> (Yates)	...	...	3,1F	...	...	...	...	under kelp on gravel bottom
<i>Ventricolaria</i> cf. <i>V.</i> <i>fordii</i> (Yates)	...	...	...	1F	...	...	...	same as above
GASTROPODS								
<i>Acteon traski</i> Stearns	...	...	1F	...	...	...	...	60-100m on sand
<i>Fusinus</i> cf. <i>F. arnoldi</i> (Cossman)	...	...	2F	...	...	...	...	30-216m near Palos Verdes
<i>Caecum</i> cf. <i>C. crebri-</i> <i>cinctum</i> (Carpenter)	...	...	2	...	...	...	...	20-70m under kelp, mainly on sand, gravel
<i>Mitrella tuberosa</i> (Carpenter)	...	...	...	3	...	...	...	14-70m on gravel
<i>Mitromorpha gracilior</i> (Tryon)	...	...	...	...	...	1	...	40-50m, on gravel under kelp
<i>Ocenebra foveolata</i> (Hinds)	...	2,1F	...	...	...	...	...	40-80m, on gravel under kelp
<i>Rissoina kelseyi</i> Dall & Bartsch	...	...	...	3	...	2	14,2F	20-50m, sand & gravel
<i>Turbonilla</i> cf. <i>T. asser</i> Dall & Bartsch	...	...	...	...	4,2F	...	...	30-150m
<i>Turbonilla</i> cf. <i>T.</i> <i>moerchi</i> Dall & Bartsch	...	...	...	...	...	...	1,3F	28-100m

lack of abrasion of some of the sublittoral fossils suggests that they have not been transported very far, and their presence in the terrace sediments may be due to upwelling conditions that prevailed along the exposed Pleistocene coastline. It may be that both wave transport and upwelling contributed the deeper sublittoral species to the upper terrace faunas.

The shallow-water character of the molluscan faunas corresponds to the low relief of the Palos Verdes terrace platforms. Where nonmarine cover is thin or deposits are exposed by excavations, the tectonically undeformed Pleistocene terrace surfaces are seen to dip gently seaward. Although the difference between the seaward edge of a given terrace and its apparent shoreline angle can be more than 35 metres, it is commonly only about 20 metres. The range of elevation of a terrace platform is usually impossible to determine because of nonmarine cover, at least 30 metres thick in places (Woodring and others 1946).

SUBSTRATE

A rocky substrate was necessary to support most of the gastropods and the epifaunal bivalves of the Palos Verdes terraces. Most of the bivalves from the upper terraces have living descendants in the coarse sand and gravel of nearby tide pools. However, gastropods such as *Acteocina culcitella* (Gould), *Alabina tenuisculpta* (Carpenter), *Assiminea californica* (Tryon), and *Sinum scopulosum* (Conrad) are evidence for at least the transitory presence of protected or semi-protected habitats with soft substrates. *Assiminea californica* (Tryon) is especially common at locality 5-1, and the small bivalve *Transenella tantilla* (Gould), common on silt and sand bottoms, was found on all of the upper terraces sampled. The limpet *Notacmaea insessa* (Hinds), found at all terrace localities but 9-1 and 12-2, lives exclusively on the brown alga *Egregia* (Burch 1945). The mollusks of the upper terraces suggest a variety of substrates during the Pleistocene similar to that found along the Palos Verdes coastline today.

LOCAL MARINE HYDROCLIMATE

Molluscan faunas of the upper terraces are generally similar to the fauna of the modern Californian province. Only four of the Pleistocene species have modern ranges that do not extend as far north as the Palos Verdes Hills (Table 3) and no northern extra-limital species are present. However, five species have their known ranges mainly to the north of the fossil localities (Table 4), whereas 25 species are presently known mainly to the south (Table 5). The upper terrace faunas are notable for their small number of extra-limital forms and their large number of predominantly southern rocky shore mollusks. All of the southern extra-limital forms are restricted to the seventh terrace; the predominantly northern and southern species are more evenly distributed among the upper terraces.

The presence of four southern extra-limital species on terrace seven, the lack of comparable northern forms, and the large number of predominantly southern exposed-shore species on most higher terraces suggests the conclusion that upper terrace faunas have a warm-water aspect, but such is not the case. Valentine and Meade (1961) noted that isotopic evidence indicates southern species in exposed-

Species in the upper terrace faunas whose modern geographic ranges do not extend as far north as the Palos Verdes Hills.

	TERRACE LOCALITIES		RANGE IN DEGREES OF NORTH LATITUDE (P. V. Hills = 33°40'N)
	7-1	7-2	
BIVALVES			
<i>Bernardina bakeri</i> Dall	18	. . .	33-25
<i>Chione picta</i> Willett	. . .	1	25-8
GASTROPODS			
<i>Acteon</i> cf. <i>A. traski</i> Stearns	1F	. . .	33-8
<i>Trivia solandri</i> Gray	1	. . .	33-25

TABLE 4

Species in the upper terrace faunas whose modern geographic ranges lie mainly to the north of the Palos Verdes Hills. F = fragment

	TERRACE LOCALITIES					RANGE IN DEGREES OF NORTH LATITUDE (P. V. Hills = 33°40'N)
	5-1	5-2	7-1	7-2	12-2	
BIVALVES						
<i>Nettastomella rostrata</i> (Valenciennes)	...	...	...	1	...	48-33
<i>Parapholas</i> cf. <i>P.</i> <i>californica</i> Conrad	...	...	10F	...	...	43-33
GASTROPODS						
<i>Acanthina spirata</i> (Blainville)	2,2F	2,1F	1	...	...	48-33
<i>Mitromorpha intermedia</i> Arnold	...	...	...	...	1	37-34
<i>Opalia montereyensis</i> Dall	...	...	1F	...	...	37-34

shore facies do not represent waters as warm as their present distributions suggest, but record isotopic paleo-temperatures fully as cool as those from associated frigidophilic species. The likelihood is that although southern exposed-shore species lived most of their lifespans at cool-water sites, they required relatively warm water at a critical stage of their early development (Valentine and Meade 1961). Such southern species may be evidence for a nearby warm-water area, perhaps a shallow coastal indentation removed from the effects of upwelling. The presence of southern extralimital mollusks on the seventh terrace only may indicate that the local warm-water area was better developed there than on the other upper terraces, or that these localities were closer to a warm-water area than those from other terraces.

Another possible explanation for the anomalous southern species in the Palos Verdes upper terrace deposits is that the pelagic larvae of subtropical Mexican species occasionally are transported northward to southern California by warm countercurrents (Woodring and others 1946; Vedder and Norris 1963; Zinsmeister 1974). Zinsmeister gave examples of modern tropical and subtropical mollusks and other invertebrates occurring far north of their known ranges, and correlated these occurrences with years when the southern countercurrent significantly raised marine temperatures along the southern California coastline. Under such conditions southern species are able to survive but not successfully reproduce in the cooler hydroclimate into which they have been transported. This could account for scattered tropical species in otherwise temperate faunas but would not account for large populations of tropical species in temperate latitudes year after year. The sparse occurrence of tropical mollusks in the upper terraces fits this hypothesis quite well. Bandy (*in* Bandy and others 1964) stated that the highest Palos Verdes terraces have a warmer water foraminiferal fauna than the lower terraces, but he did not document this.

TABLE 5

Species in the upper terrace faunas whose modern geographic ranges lie mainly to the south of the Palos Verdes Hills. F = fragment

	TERRACE LOCALITIES					RANGE IN DEGREES OF NORTH LATITUDE (P. V. Hills = 33°40'N)	
	5-1	5-2	7-1	7-2	9-1	12-1	12-2
BIVALVES							
<i>Pristes</i> cf. <i>P. oblonga</i> (Carpenter)	...	...	...	...	4	...	...
<i>Semele</i> cf. <i>S. decisa</i> Conrad	...	...	6F	...	...	...	...
GASTROPODS							
<i>Alabina tenuisculpta</i> (Carpenter)	...	...	...	...	...	1	...
<i>Alvinia cosmia</i> Bartsch	...	...	...	8	...	...	...
<i>Alvinia oldroydae</i> Bartsch	...	...	...	...	...	...	2
<i>Astraea undosa</i> (Wood)	...	...	1, 1F	...	...	...	...
<i>Bitium armillatum</i> Carpenter	2, 2F	...	...	...	...	...	...
<i>Caecum dalli</i> Bartsch	...	...	...	13, 7F	...	...	...
<i>Caecum</i> cf. <i>C. dalli</i> Bartsch	...	...	...	...	...	...	1
<i>Cerastostoma nuttalli</i> (Conrad)	...	...	1, 1F	...	...	1	...
<i>Cerithium sculptum</i> Sowerby	56, 10F	12, 12F	...	...	...	...	...
<i>Crepidula coei</i> Berry	2	...	...	...	...	...	...
<i>Cypraea spadicea</i> Swainson	...	...	3, 2F	...	...	2F	...
<i>Fartulum orcutti</i> (Dall)	...	...	...	...	...	...	11
<i>Maxwellia gemma</i> (Sowerby)	...	...	1	...	...	1	...
<i>Metaxia convexa</i> (Carpenter)	...	...	...	...	...	1F	...
<i>Odostomia aepynota</i> Dall & Bartsch	...	...	...	1	...	...	...
<i>Odostomia</i> cf. <i>O. aepynota</i> Dall & Bartsch	...	...	...	...	...	...	1

TABLE 5 (continued)

Species in the upper terrace faunas whose modern geographic ranges lie mainly to the south of the Palos Verdes Hills. F = fragment

<i>Odostomia</i> cf. <i>O. helga</i>	...	...	...	...	1	...	...	34-33
Dall & Bartsch								
<i>Odostomia</i> aff. <i>O. hemphilli</i>	...	...	...	...	2	...	...	34-27
Dall & Bartsch								
<i>Odostomia</i> cf. <i>O. lucca</i>	...	...	...	...	4	...	...	34-33
Dall & Bartsch								
<i>Odostomia navisa</i> Dall & Bartsch	...	...	...	4	...	...	1	34-28
<i>Odostomia turricula</i>								
Dall & Bartsch	1	...	...	1	...	...	...	34-31
<i>Petalocochnus</i> cf. <i>P. macrophragma</i> Carpenter	...	...	...	1F	...	...	...	34-5
Rissoina dalli Bartsch	...	...	...	...	1	...	...	34-33
<i>Rissoina kelseyi</i> Dall & Bartsch	...	...	...	3	...	2	14,2F	34-33
<i>Tegula gallina multiflora</i> (Stearns)	4F	3,1F	13,3F	3F	...	19,97F	2,1F	34-8

The five species on the upper terraces that have predominantly northern modern ranges were found on terraces five, seven, and twelve, supporting the general cool-water aspect of the upper terrace faunas. The dominant cool-water aspect of the upper terrace faunas, with the presence of a small southern element, agrees well with the thermal environment of the southern California Pleistocene as reconstructed by Valentine (1961) and others.

The faunas of upper terraces described here are similar in most respects to the faunas of the lower terraces. The fauna on the lowest subaerial terrace, which has been thoroughly studied, is an association of warm-water mollusks representing deposition at protected sites and cool-water mollusks representing exposed rocky and sandy habitats. Woodring and others (1946) noted that the upper terraces seemed to have a fairly uniform faunal facies made up of mollusks known from tide pools and shallow subtidal habitats and designated this the "rock-cliff and tide-pool facies." This facies was observed to be dominant above the fourth terrace and prevalent at lower elevations, where a few mollusks from protected and semi-protected habitats were known. From terraces four, five, and six, Valentine (1962) recognized essentially the same molluscan associations as had Woodring and his coworkers (1946), with a small number of additional species representative of a sandy substrate in near proximity to an exposed rocky shore. The 47 species added to the Palos Verdes Hills terraces in this report more firmly establish the predominance of the "rock-cliff and tide-pool facies" in the upper terrace deposits, since all of these added species are found living in the intertidal or shallow subtidal zones of exposed shores or in closely adjacent habitats. The specimens of *Bernardina bakeri* Dall, *Chione picta* Willett, *Acteon* cf. *A. traski* Stearns, and *Trivia solandri* Gray from terrace seven (Table 3) extend the known range of the southern rocky shore element slightly backward in time, as this element had previously been known only as high as terrace five (Valentine 1962).

The upper terrace deposits represent a hydroclimate similar to that of the lowest terrace beds (the "Palos Verdes Sand" of most earlier workers) and other lower terrace deposits, but a narrower range of environments. The broader terrace platforms and more extensive coastlines developed on the lower terraces were probably responsible for the more diverse molluscan communities that occurred there.

AGE AND CORRELATION

The precise age of the terrace deposits in the Palos Verdes Hills is still in doubt. The deposits on the lowest emergent terrace are of undoubted late Pleistocene age (Woodring and others 1946; Valentine 1961), but uncertainty as to age assignment increases for progressively higher terraces. Woodring and others (1946) considered all of the present Palos Verdes terraces to have been cut during the late Pleistocene. However, they also thought that lower Pleistocene terrace deposits had once been formed and subsequently removed during formation of the present terrace deposits, and that the time interval between deposition of the lower Pleistocene formations in San Pedro and the terrace deposits was approximately equal to the middle third of the Pleistocene. Some later workers have considered the terrace deposits to be

of slightly greater age. Wahrhaftig and Birman (1965) noted that the water depths suggested by the molluscan facies of the lower Pleistocene formations around the base of the hills made it possible for some of the highest terraces to be contemporaneous with these units, but Poland and Piper (1956) considered the 12 upper terraces to be only partly correlative with unnamed upper Pleistocene deposits in the Long Beach-Santa Ana area. Bandy (*in* Bandy and others 1964) considered the highest Palos Verdes terraces to be of early Pleistocene or late Pliocene age because they exhibited a warmer water foraminiferal fauna than the lower terraces, although this was not documented. Only two extinct molluscan taxa are known from the higher terraces, whereas 49 are found in the nearby lower Pleistocene beds in San Pedro.

More precise age estimates for the terraces have been attempted by several workers, usually based on detailed analysis of the temperature facies shown by molluscan fossils. Late Pleistocene deposits at Newport Bay were correlated with the fauna of the lowest Palos Verdes terrace by Kanakoff and Emerson (1959) and referred to a time interval later than early Pleistocene and prior to the Wisconsin Glaciation. An Illinoian age has been suggested for lower terrace deposits throughout southern California and Baja California (Hubbs 1960). The modern aspect of the mollusks in the beds of the lowest Palos Verdes terrace and the relatively late occurrence of these deposits in the sequence of Pleistocene events of the Los Angeles Basin suggested an early Wisconsin age to Valentine (1961). Noting the lack of southern mollusks on terraces above the fourth, however, Valentine admitted that such higher terraces could represent earliest Wisconsin or even late Sangamon time. The discovery of four extra-limital southern species on terrace seven during this study does not modify Valentine's suggested age, as these four species are of the rocky shore southern facies, which has been shown to yield isotopic paleotemperatures fully as low as strictly northern mollusks (Valentine and Meade 1961), and a warmer hydroclimate is not required to explain their presence.

The terrace mollusks at Punta China, Baja California, are thought to be of late Pleistocene age on faunal and stratigraphic grounds and are similar to the terrace faunas above the first terrace at Palos Verdes (Emerson 1956). Terrace faunas on the southern California islands are much like those of the Palos Verdes Hills. Their ages and suggested correlations with the mainland deposits are divisible into two groups: terraces at about 30 metres elevation and lower have molluscan faunas virtually identical to those of upper Pleistocene mainland deposits; terrace faunas at higher levels seem to be older (Valentine and Lipps 1967). These higher terraces contain a well-defined extinct element of mollusk species such as *Calicantharus fortis* (Carpenter), *Crepidula princeps* Conrad, *Arca sisquocensis* Reinhart, and *Humilaria perlamino* (Conrad), and the echinoid *Dendraster venturaensis* Kew. Island terraces bearing these extinct species range in elevation from about 45 metres to 270 metres. These species suggest that the upper island terraces are older than the upper Pleistocene deposits of the mainland, though they are insufficient evidence to support a definite older age for these terraces (Valentine and Lipps 1967). Vedder and Norris (1963) attributed the presence of these taxa to the survival of a relict fauna on the islands, not to an early Pleistocene age. No such

extinct element occurs on the Palos Verdes or other mainland terraces, which suggests either that the marine hydroclimate between the two regions was different, or that the islands were tectonically uplifted before the mainland coast. Since the southern Channel Islands are clearly within the late Pleistocene Verdean molluscan province (Valentine and Lipps 1967), it would be reasonable to expect the mainland and islands to have shared the same Pleistocene fauna. However, differences between the islands and mainland are known for the modern molluscan faunas (Strong 1923), including the presence of the islands of both northern and southern species that are absent on the mainland (Lipps 1967), and this situation might have prevailed during much or all of the Pleistocene. Even though the Palos Verdes Hills formed an island during the Pleistocene, it was only about 10-15 miles (16-24 kilometres) from the mainland, but at least 50 miles (82 kilometres) from the other islands that now have fossiliferous Pleistocene deposits. Molluscan faunal differences between the Palos Verdes island and the other Pleistocene islands were certainly possible. As differences in the tectonic histories of the Channel Islands and the present mainland are still not known with certainty, faunal differences between the upper terraces of the islands and the mainland cannot yet be definitely attributed to either environmental or tectonic causes. If the differences are environmental, the groups of mainland and island terraces cannot be correlated. If they are tectonic, all of the Palos Verdes terraces are younger than the higher island terraces and doubtless of late Pleistocene age.

A number of radiometric dates are available from southern California Pleistocene terrace deposits (Kulp and others 1952; Fanale and Schaeffer 1965; Szabo and Rosholt 1969; Szabo and Vedder 1971), primarily on the mainland. They do not clarify the terrace chronology based on faunal evidence. There is wide discordance among such dates and they will remain in doubt until more reliable methods of dating mollusk shells are developed. In general, however, radiometric ages for the lowest Palos Verdes Hills terrace range from about 70,000 to 130,000 years, whereas those for terrace twelve indicate an age greater than about 360,000 years.

The Palos Verdes Hills upper terraces are considered here to be of late Pleistocene age. The modern character of the faunas and absence of the extinct faunal element present on the higher terraces of the southern California islands suggests faunal equivalence of the entire Palos Verdes terrace sequence with the lower island terraces. It seems to exclude a Pliocene or early Pleistocene age for any of the Palos Verdes Hills terraces. The inferred cool-water character of the upper terrace molluscan faunas also does not support a Pliocene age for the upper terrace deposits.

SUMMARY

The molluscan faunas of the Palos Verdes Hills upper terraces are similar in many ways to the more extensively studied faunas of the lower terraces. They represent the same range of environments as the lower terrace faunas, but contain mainly species from an exposed rocky shore habitat. Very few species from protected or semiprotected habitats occur in the upper terrace deposits, suggesting that such

habitats were quite restricted or perhaps transitory. In this respect, the Palos Verdes island of Pleistocene time might have been like the present southern California islands, where semiprotected coves with sandy or silty bottoms indent rugged coastlines. The shallowness of the sites of deposition is indicated by the gentle seaward slope of the terrace platforms and by the molluscan faunas. Numerous intertidal species occur in the terrace deposits, and the greatest modern depth limits of most of the shallow inner sublittoral mollusks occur between 20 and 40 metres. It is likely that most of the terrace deposits were laid down within a depth range of 0 to 30 metres, although depositional sites on the margin of a rising landmass would naturally contain organic remains from several depth zones. The sites of deposition might have been somewhat deeper than indicated by analogy with modern depth limits of the fossil mollusks if there was upslope migration due to the cooler Pleistocene hydroclimate.

The upper terrace molluscan faunas suggest a greater range of water temperatures than prevails today along the Palos Verdes Hills coastline, and a generally lower sea surface temperature. The rocky shore species that predominate in the terrace deposits, whether of northern or southern affinity, suggest cool water. Valentine and Meade (1961) showed with oxygen isotope studies that both southern and northern rocky shore mollusks yield low isotopic paleotemperatures. A few species present in the terrace deposits live today only in tropical waters to the south. These lived in protected warm-water sites or were introduced occasionally by warm southern countercurrents.

The entire terrace sequence is considered to be of late Pleistocene age as suggested by the modern aspect of the mollusks. There is only one extinct species, the gastropod *Rissoina pleistocena* Bartsch, found on terrace nine. The upper terrace faunas are virtually identical to the lower terrace faunas of accepted late Pleistocene age. Several extinct species of mollusks and an extinct echinoid of late Pliocene and early Pleistocene age present on the upper terraces of the southern California islands are absent in the Palos Verdes Hills. Although molluscan evidence for a pre-late Pleistocene age for the Palos Verdes Hills terrace sequence is lacking, faunal grounds are often unreliable for accurate age estimates within an epoch as brief as the Pleistocene. Precise age determinations must await more reliable radiometric measurements.

TABLE 6

Mollusks from upper terraces of the Palos Verdes Hills, showing number of specimens or valves from each locality. F= fragment

	TERRACE LOCALITIES						
	5-1	5-2	7-1	7-2	9-1	12-1	12-2
BIVALVES							
<i>Mytilus</i> sp.	...	...	...	1F	1	...	2
<i>Septifer bifurcatus</i> (Conrad)	...	...	1, 1F	2	2, 5F	14, 27F	6, 7F
<i>Modiolus</i> sp.	2F	1	...	8F	...	...	...
<i>Lithophaga</i> sp.	...	...	3	...	5	...	...
<i>Ostrea</i> cf. <i>O. lurida</i> Carpenter	...	...	1	...	...	...	...
<i>Ostrea</i> sp.	...	...	...	...	1F	...	...
<i>Hinnites multirugosus</i> (Gale)	...	...	2, 2F	...	...	...	...
<i>Pecten</i> sp.	...	...	...	1F	...	...	...
<i>Pododesmus macrochismus</i> (Deshayes)	...	...	1	...	...	...	...
<i>Chama pellucida</i> Broderip	...	...	7, 2F	2	1	...	1
<i>Glans subquadrata</i> (Carpenter)	1, 2F	2	1	11, 3F	62	16	32
<i>Milneria kelseyi</i> Dall	1	...	...	...	...	...	...
<i>Milneria</i> cf. <i>M. minima</i> Dall	...	...	1	1	...	...	...
<i>Bernardina bakeri</i> Dall	...	...	18	...	...	...	...
<i>Lasaea cistula</i> Keen	...	...	1	...	...	...	...
<i>Lasaea subviridus</i> Dall	12	...	...	...	...	...	...
<i>Lasaea</i> cf. <i>L. subviridus</i> Dall	...	...	...	7	3	...	1
<i>Pristes oblonga</i> (Carpenter)	...	...	...	...	4	...	...
<i>Epilucina californica</i> (Conrad)	18, 5F	3	8, 2F	2F	437, 143F	19, 10F	3, 1F
<i>Lucinoma annulata</i> Reeve	1F	...	...	...	...	...	...
<i>Diplodonta</i> cf. <i>D. sericata</i> (Reeve)	...	...	1	...	...	...	...
<i>Chione picta</i> Willett	...	...	...	1	...	...	...
<i>Chione</i> sp.	1F	...	...	...	...	...	...
<i>Cumingia californica</i> Conrad	...	...	...	1F	...	...	...
<i>Cumingia</i> cf. <i>C. californica</i> Conrad	...	...	...	...	1F	...	...
<i>Cumingia lamellosa</i> Sowerby	...	...	1	...	...	...	...
<i>Semele</i> cf. <i>S. decisa</i> (Conrad)	...	...	6F	...	...	...	...
<i>Semele incongrua</i> Carpenter	...	...	...	...	1F	...	...

TABLE 6 (cont'd)

Mollusks from upper terraces of the Palos Verdes Hills, showing number of specimens or valves from each locality. F = fragment.

	TERRACE LOCALITIES						
	5-1	5-2	7-1	7-2	9-1	12-1	12-2
BIVALVES (cont'd)							
<i>Semele rupicola</i> Dall	...	...	1F	...	...	...	...
<i>Semele</i> sp.	...	...	...	...	...	...	1F
<i>Corbula luteola</i> Carpenter	...	...	1	...	...	...	...
<i>Ventricularia fordii</i> (Yates)	...	...	3,1F	1F	...	...	...
<i>Transenella tanilla</i> (Gould)	20	1	6	16	1	...	2
<i>Saxidomus nuttalli</i> Conrad	...	...	2,3F	...	...	...	...
<i>Penitella</i> sp.?	...	...	...	1F	...	...	...
<i>Parapholas</i> cf. <i>P. californica</i> Conrad	...	...	10F	...	...	...	...
<i>Netastomella rostrata</i> (Valenciennes)	...	...	...	1	...	...	...
GASTROPODS							
<i>Haliotis cracherodii</i> Leach	...	...	...	...	...	13,131F	4F
<i>Haliotis rufescens</i> Swanson	...	...	...	...	...	1	...
<i>Haliotis</i> sp.	11F	...	...	...	19F	...	4F
<i>Diodora arnoldi</i> McLean	...	...	...	...	...	1	3
<i>Megathura crenulata</i> (Sowerby)	...	...	1	...	...	...	...
<i>Megatebennus bimaculatus</i> (Dall)	...	...	...	...	...	...	3,1F
<i>Lucapinella callomarginata</i> (Dall)	...	...	...	...	...	1F	...
<i>Fissurella volcano</i> Reeve	...	...	...	...	...	19,30F	17,14F
<i>Acmaea mitra</i> Eschscholtz	2	...	16,1F	12,2F	4	...	...
<i>Acmaea</i> cf. <i>A. mitra</i> Eschscholtz	...	...	...	...	...	...	1
<i>Collisella edmitchelli</i> (Lipps)	...	...	...	3	...	13,5F	5
<i>Collisella</i> cf. <i>C. edmitchelli</i> (Lipps)	...	...	...	...	...	...	4
<i>Collisella limatula</i> (Carpenter)	19,12F	...	17,7F	8	...	20	3
<i>Collisella</i> cf. <i>C. limatula</i> (Carpenter)	...	...	...	...	1,1F	...	...
<i>Collisella pelta</i> (Rathke)	5	1	...	...	...	...	...
<i>Collisella</i> cf. <i>C. pelta</i> (Rathke)	4	...	...	...	...	1,1F	...
<i>Collisella scabra</i> (Gould)	4	1	9,1F	4,3F	9,3F	26,8F	44,4F

<i>Collisella</i> sp.	...	...	...	...	...	...	...	...	...
<i>Notamea inessa</i> (Hinds)	6,3F	...	6	...	7	...	...	2	...
<i>Notamea paleacea</i> (Gould)	1	...	...	...	...	...	...	...	...
<i>Lirularia</i> cf. <i>L. acuticostata</i> (Carpenter)	...	...	...	...	...	...	...	...	1
<i>Lirularia succincta</i> (Carpenter)	1	...	...	...	...	...	...	...	...
<i>Lirularia</i> cf. <i>L. succincta</i> (Carpenter)	...	...	...	...	1	...	...	...	...
<i>Norrisia norrisi</i> (Sowerby)	1F	...	36,4F	...	3,2F	...	...	...	...
<i>Tegula funebris</i> (A. Adams)	7,6F	...	1F	...	...	...	...	...	...
<i>Tegula gallina multiflora</i> (Stearns)	3,5F	...	13,3F	...	3F	...	...	19,97F	2,1F
<i>Tegula eiseni</i> (Jordan)	...	...	3	...	...	3	...	...	...
<i>Parviturbo acuticostata</i> (Carpenter)	...	...	...	...	1	...	...	3	8
<i>Liotia fenestrata</i> Carpenter	...	...	...	...	...	...	...	...	3
<i>Homalopoma baculum</i> (Carpenter)	7	...	...	...	...	...	...	...	...
<i>Homalopoma</i> cf. <i>H. baculum</i> (Carpenter)	2	...	...	...	...	...	...	...	...
<i>Homalopoma fenestratum</i> (Dall)	...	...	...	...	...	...	...	4	5,1F
<i>Homalopoma luridum</i> (Dall)	10,4F	...	1,1F	...	12,1F	...	...	4,5F	8
<i>Asraea undosa</i> (Wood)	...	...	1,1F	...	...	...	...	...	...
<i>Tricolia pulloides</i> (Carpenter)	...	...	...	...	...	...	...	1	...
<i>Tricolia</i> aff. <i>T. pulloides</i> (Carpenter)	...	...	...	...	...	...	...	1	...
<i>Tricolia</i> sp.	...	...	...	...	16	1	...	...	16
<i>Lacuna unifasciata</i> Carpenter	...	...	...	...	4	...	...	3	1
<i>Lacuna</i> cf. <i>L. unifasciata</i> Carpenter	2	...	...	...	...	1	...	...	...
<i>Lacuna</i> sp.	3	...	...	...	...	...	...	...	2
<i>Littorina planaxis</i> Philippi	6,1F	...	3	...	16	2F	...	71,16F	22
<i>Littorina scutulata</i> Gould	401,18F	...	8,2F	...	36,2F	4	...	72,15F	33,3F
<i>Alvinia aequisculpta</i> (Keep)	...	...	...	...	...	...	...	...	9,3F
<i>Alvinia</i> cf. <i>A. carpenteri</i> (Weinkauff)	...	...	...	...	5	...	...	...	...
<i>Alvinia compacta</i> (Carpenter)	...	...	3	...	1	...	...	...	28,1F
<i>Alvinia cosmia</i> (Bartsch)	...	...	...	...	8	...	...	...	...
<i>Alvinia oldroydae</i> (Bartsch)	...	...	...	...	...	...	...	...	...
<i>Alvinia purpurea</i> (Dall)	...	...	2	...	16	...	...	...	2
<i>Alvinia</i> sp.	...	...	...	...	...	1	...	1	124,5F
<i>Barleeia</i> cf. <i>B. haliotiphila</i> Carpenter	...	...	...	...	...	40	...	...	5
<i>Barleeia</i> cf. <i>B. subreus</i> Carpenter	...	...	...	...	...	...	...	...	2
<i>Rissoina dalli</i> Bartsch	...	...	...	...	...	...	...	...	10
	...	...	...	...	...	1	...	...	...

TABLE 6 (cont'd)

Mollusks from upper terraces of the Palos Verdes Hills, showing number of specimens or valves from each locality. F = fragment

	TERRACE LOCALITIES						
	5-1	5-2	7-1	7-2	9-1	12-1	12-2
GASTROPODS (cont'd)							
<i>Rissoina kelseyi</i> Dall & Bartsch	...	...	...	3	...	2	14,2F
<i>Rissoina pleistocena</i> Bartsch	...	...	...	...	4,4F	...	...
<i>Assiminea californica</i> (Tryon)	22	...	...	...	...	3	...
<i>Teinostoma supravallata</i> (Carpenter)	...	...	...	59	167	2	121
<i>Caecum californicum</i> Dall	...	...	...	47,10F	9,1F	...	...
<i>Caecum</i> cf. <i>C. crebricinctum</i> Carpenter	...	...	2	...	...	...	...
<i>Caecum dalli</i> Bartsch	...	...	...	13,7F	...	...	...
<i>Caecum</i> cf. <i>C. dalli</i> Bartsch	...	...	...	...	...	...	...
<i>Caecum</i> sp.	...	...	...	3,2F	...	...	...
<i>Fartulum occidentale</i> Bartsch	...	...	...	2	42	...	20,1F
<i>Fartulum</i> cf. <i>F. occidentale</i> Bartsch	...	...	...	...	...	...	1
<i>Fartulum orcutti</i> (Dall)	...	...	46F	...	...	...	11
<i>Serpulorbis squamigerus</i> Carpenter	...	...	...	...	...	41F	2F
<i>Petalocochnus macrophragma</i> Carpenter	...	...	...	1F	...	...	...
<i>Petalocochnus montereyensis</i> Dall	3F	...	...	...	...	...	7F
<i>Petalocochnus</i> cf. <i>P. montereyensis</i> Dall	...	1F	...	2F	4F	...	...
<i>Cerithium sculptum</i> Sowerby	68,10F	9,12F	...	...	...	...	...
<i>Alabina tenuisculpta</i> (Carpenter)	...	...	...	...	...	1	...
<i>Alabina</i> cf. <i>A. tenuisculpta</i> (Carpenter)	...	...	...	...	...	...	1
<i>Bititium armillatum</i> Carpenter	2,2F	...	...	...	...	...	...
<i>Bititium</i> cf. <i>B. armillatum</i> Carpenter	2	...	...	...	...	...	23
<i>Bititium</i> cf. <i>B. attenuatum</i> Carpenter	2	...	...	2	...	...	1
<i>Bititium purpureum</i> (Carpenter)	1	...	...	...	...	...	...
<i>Bititium</i> aff. <i>B. purpureum</i> (Carpenter)	...	...	...	...	...	...	...
<i>Cerithiopsis</i> sp.	2,2F	...	3	10	1	50	41
<i>Metaxia convexa</i> Carpenter	...	...	...	1	...	1F	3,1F
<i>Metaxia</i> sp.	...	...	...	...	...	...	2
<i>Seila montereyensis</i> Bartsch	...	...	...	1	2	...	4,2F

<i>Triphora pedroana</i> Bartsch	...	1F	1,2F	...	1,6F	4,4F
<i>Triphora</i> cf. <i>T. pedroana</i> Bartsch	...	...	...	...	...	4,4F
<i>Epitonium</i> sp.	...	...	3	...	...	1F
<i>Opalia</i> sp.	...	1F	...	...	1F	...
<i>Balcis micans</i> (Carpenter)	...	...	1	...	...	...
<i>Balcis</i> cf. <i>B. thersites</i> (Carpenter)	...	...	1F	...	...	2
<i>Balcis</i> sp.	...	1	...	...	...	1
<i>Hipponix antiquatus</i> (Linnaeus)	16,3F	2	59	8,1F	131,5F	16
<i>Hipponix tumens</i> Carpenter	...	14	26	...	16,5F	56
<i>Crepidula adunca</i> Sowerby	1F	...	...	...	...	...
<i>Crepidula</i> cf. <i>C. adunca</i> Sowerby	1	...	...	...	...	...
<i>Crepidula coei</i> Berry	2	...	...	...	...	...
<i>Crepidula</i> cf. <i>C. coei</i> Berry	...	...	3	...	...	...
<i>Crepidula nummaria</i> Gould	...	3,2F	1	...	1	...
<i>Crepidula onyx</i> Sowerby	...	1	...	...	2	...
<i>Crepidula</i> cf. <i>C. onyx</i> Sowerby	3	...	...	...	...	...
<i>Crepidula</i> sp.	...	...	1	...	...	36
<i>Crepidatella lingulata</i> (Gould)	...	5,1F	...	...	5,2F	4
<i>Sinum scopulosum</i> (Conrad)	...	...	...	...	...	1F
<i>Trivia solandri</i> (Sowerby)	...	1	...	...	...	...
<i>Cypraea spadicea</i> Swainson	...	3,2F	...	...	2F	...
<i>Cymatium</i> sp.	1F	...	...	...	...	...
<i>Ceratostoma nuttalli</i> (Conrad)	...	1,1F	...	...	1	...
<i>Ocenebra foveolata</i> (Hinds)	...	2,1F	...	...	...	...
<i>Ocenebra interfossa</i> (Carpenter)	...	...	3	...	...	...
<i>Ocenebra lurida</i> (Middendorff)	2	...	...	...	...	...
<i>Ocenebra gemma</i> (Sowerby)	1	...	...	...	...	...
<i>Maxwellia gemma</i> (Sowerby)	...	1	...	...	1	...
<i>Acanthina spirata</i> (Blainville)	2,2F	2,1F	1	...	...	...
<i>Macron lividus</i> (A. Adams)	...	...	2	...	...	...
<i>Amphissa versicolor</i> Dall	1	...	2,2F	3,2F	7F	1,3F
<i>Amphissa</i> cf. <i>A. versicolor</i> Dall	...	...	...	...	...	...
<i>Mitrella carinata</i> (Hinds)	13,3F	6,1F	1	6,1F	1F	...
<i>Mitrella tuberosa</i> (Carpenter)	...	...	3	3	...	...
<i>Nassarina penicillata</i> (Carpenter)	...	...	8	8	...	...

TABLE 6 (cont'd)

Mollusks from upper terraces of the Palos Verdes Hills, showing number of specimens or valves from each locality. F = fragment

	TERRACE LOCALITIES						
	5-1	5-2	7-1	7-2	9-1	12-1	12-2
GASTROPODS (cont'd)							
<i>Nassarius fossatus</i> (Gould)	...	...	...	1	...	...	...
<i>Nassarius mendicus</i> (Gould)	3,2F	2	2F	...	...	1	...
<i>Fusus</i> cf. <i>F. arnoldi</i> (Cossman)	...	...	...	...	...	...	2
<i>Mitra</i> cf. <i>M. idae</i> Melvill	...	...	...	...	...	...	...
<i>Volvarina taeniolata</i> Mörch	...	...	...	...	...	1	...
<i>Granula subrigona</i> (Carpenter)	1	...	...	9	2,1F	...	...
<i>Granulina margaritula</i> (Carpenter)	...	...	...	5	3	...	5,1F
<i>Olivella</i> cf. <i>O. baetica</i> Carpenter	...	...	...	1F	...	...	...
<i>Olivella buplicata</i> (Sowerby)	14,2F	2	8,1F 69,17F	...	...	...	...
<i>Conus californicus</i> Hinds	...	...	...	5,3F	2F	9,12F	3,3F 1F
<i>Mitromorpha aspera</i> (Carpenter)	...	...	...	...	...	1	...
<i>Mitromorpha gracilior</i> (Tryon)	...	...	...	...	...	...	1
<i>Mitromorpha intermedia</i> Arnold	...	...	...	...	...	...	4,1F
<i>Clathromangilia interfossa</i> (Carpenter)	1	...	...	...	...	...	...
<i>Clathromangilia</i> cf. <i>C. interfossa</i> (Carpenter)	1	1	...	...	...	...	1F
<i>Clathromangilia variegata</i> Carpenter	...	...	...	...	...	...	...
<i>Clathromangilia</i> cf. <i>C. variegata</i> (Carpenter)	...	...	...	1,1F	...	...	...
<i>Clathromangilia</i> aff. <i>C. variegata</i> (Carpenter)	...	...	1	...	...	1	...
<i>Clathromangilia</i> sp.	2	...	...	...	...	...	1
<i>Acteon traski</i> Stearns	...	...	1F	...	...	...	...
<i>Acteocina culcitella</i> (Gould)	1	...	...	...	...	...	...
<i>Acteocina</i> sp.?	...	...	...	...	...	...	1F
<i>Acteocina</i> cf. <i>A. harpa</i> (Dall)	...	...	...	1,2F	...	...	...
<i>Odostomia aepynota</i> Dall & Bartsch	...	...	...	1	...	...	...
<i>Odostomia</i> cf. <i>O. aepynota</i> Dall & Bartsch	...	...	...	...	...	...	1
<i>Odostomia</i> cf. <i>O. helga</i> Dall & Bartsch	...	...	...	...	1	...	...
<i>Odostomia</i> aff. <i>O. hemphilli</i> Dall & Bartsch	...	...	...	...	2	...	...
<i>Odostomia</i> cf. <i>O. lucca</i> Dall & Bartsch	...	...	...	...	4	...	...

<i>Odostomia navisa</i> Dall & Bartsch	...	...	...	4	...	...	...
<i>Odostomia</i> cf. <i>O. trachis</i> Dall & Bartsch	...	...	...	9	...	...	...
<i>Odostomia turricula</i> Dall & Bartsch	1	...	...	1	...	...	...
<i>Odostomia</i> sp.	...	...	...	...	1	...	2
<i>Turbonilla</i> cf. <i>T. asser</i> Dall & Bartsch	...	...	...	...	4,2F	...	1
<i>Turbonilla</i> cf. <i>T. moerchi</i> Dall & Bartsch	...	...	...	...	...	...	1,3F
<i>Turbonilla</i> sp.	...	...	...	3,1F	...	...	4
<i>Trimusculus reticulatus</i> (Sowerby)	...	...	...	...	...	1	2
CHITONS							
<i>Lepidochitona keepiana</i> Berry	...	...	1	...	1	...	...
<i>Nuttallina californica</i> (Reeve) or <i>N. fluxa</i> Carpenter	...	...	...	...	6	23	...
<i>Nuttallina</i> sp.	...	...	...	1	5	5	...
<i>Chaetopleura gemma</i> Carpenter	...	...	1	...	...	1	1
<i>Mopalia</i> aff. <i>M. ciliata</i> (Sowerby)	1	...	1	...	...	...	...
<i>Mopalia</i> cf. <i>M. lowei</i> Pilsbry	...	...	...	2	...	...	...
<i>Mopalia muscosa</i> (Gould)	3	2	2	1	...	1	...
<i>Mopalia wosnessenski</i> Middendorff	...	...	...	...	...	...	...
<i>Mopalia</i> cf. <i>M. wosnessenski</i> Middendorff	1	1	...	...	...	...	...
<i>Mopalia wosnessenski</i> Middendorff or <i>M. hindsii</i> (Sowerby)	1	...	...	...	...	...	1
<i>Mopalia</i> sp.	...	...	...	...	...	...	...
<i>Placiphorella velata</i> Carpenter	...	...	1	...	...	...	...
<i>Callistochiton crassicaudatus</i> Pilsbry	...	...	1	8	...	10	27
<i>Callistochiton decoratus</i> Pilsbry	...	...	2	3	...	2	2
<i>Callistochiton palmulatus</i> Carpenter	...	...	1	3	...	4	...
<i>Callistochiton</i> sp.	...	...	...	...	...	2	...
<i>Stenoplax heathiana</i> Berry	1	1	...	...	...	1	2
<i>Stenoplax heathiana</i> Berry or <i>S. fallax</i> Carpenter	1	...	...	...	...	...	...
<i>Stenoplax</i> cf. <i>S. magdalenensis</i> (Hinds)	...	...	8	4	6	...	...
<i>Stenoplax</i> sp.	1	...	...	...	...	...	...

REGISTER OF LOCALITIES

LACMIP = Natural History Museum of Los Angeles County, Invertebrate Paleontology Section, where collections made for this study are housed.

Loc. 5-1 (LACMIP loc. 1309). Terrace five. Road cut on east side of Via Buena, opposite a fire hydrant about 60 metres north of the intersection with Via Victoria. Lies 480 metres (1,600 feet) N. 16° E. from bench mark 273. Elevation 123 metres (410 feet). Collected by W. H. Easton and L. Marinovich.

Loc. 5-2 (LACMIP loc. 1310). Terrace five. Road cut at the intersection of Dauntless Drive and Conqueror Drive. Lies 474 metres (1,580 feet) N. 89° E. from bench mark 320. Elevation 146 metres (485 feet). Collected by W. H. Easton and L. Marinovich.

Loc. 7-1 (LACMIP loc. 1307). Terrace seven. Building excavation 582 metres (1,940 feet) N. 4° W. from bench mark 382. Elevation 192 metres (640 feet). Collected by W. H. Easton and L. Marinovich.

Loc. 7-2 (LACMIP loc. 1308). Terrace seven. Same building excavation as locality 7-1, but 30 metres farther south along the excavation cut from the Pleistocene sea cliff. Lies 550 metres (1,850 feet) N. 8° W. from bench mark 382. Elevation 192 metres (640 feet). Collected by W. H. Easton and L. Marinovich.

Loc. 9-1 (LACMIP loc. 1306). Terrace nine. Building excavation 1,470 metres (4,900 feet) N. 69° E. from bench mark 273. Elevation 254 metres (847 feet). Collected by W. H. Easton and L. Marinovich.

Loc. 12-1 (LACMIP loc. 1304). Terrace twelve. Road cut on north side of Crest Road, 525 metres (1,750 feet) S. 60° E. from triangulation station on San Pedro Hill. Equivalent to locality 75 of Woodring and others (1946). Elevation 365 metres (1,215 feet). Collected by W. H. Easton.

Loc. 12-2 (LACMIP loc. 1305). Terrace twelve. Road cut on north side of Crest Road, 405 metres (1,356 feet) S. 14° E. from triangulation station on San Pedro Hill. The first road cut downhill along Crest Road from locality 12-1. Elevation 360 metres (1,200 feet). Collected by W. H. Easton and L. Marinovich.

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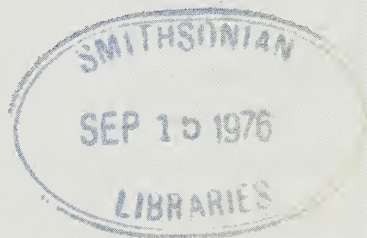
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A REVIEW OF THE
SWIFTS OF THE GENUS *HIRUNDAPUS* (AVES: APODIDAE)

By CHARLES T. COLLINS AND RICHARD K. BROOKE

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

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A REVIEW OF THE
SWIFTS OF THE GENUS *HIRUNDAPUS* (AVES: APODIDAE)¹

By CHARLES T. COLLINS² AND RICHARD K. BROOKE³

DEDICATION

This paper is dedicated to the memory of Dr. David Lack in recognition of his substantial contributions to our present knowledge of the biology of swifts.

ABSTRACT: A review of the literature on the large east Asiatic swifts of the genus *Hirundapus* as well as new data on their osteology indicates that the genus consists of four species (*caudacutus*, *cochinchinensis*, *giganteus*, and *celebensis*) and is generically separable from *Chaetura*. Subspecies limits are reviewed. The typical nest site of *Hirundapus* swifts is a scrape in the detritus at the bottom of hollow trees. Other reported nest sites are largely atypical or attributable to other species. The available information on plumages, body weight, nests, eggs, clutch size, food and behavior are summarized. The common name Needletail is proposed for the genus.

INTRODUCTION

The swifts of the avian family Apodidae are extremely difficult to study under field conditions. Their great mobility and speed of flight preclude periods of prolonged observation and their nest sites, if known, are often in inaccessible holes in trees or rocky crevices. This has led to an accumulation of anecdotal information about species, some based on actual observation, some on hearsay. Often the

¹REVIEW COMMITTEE FOR THIS CONTRIBUTION

LUIS F. BAPTISTA
HERBERT FRIEDMANN
KENNETH E. STAGER

²Research Associate in Ornithology, Natural History Museum of Los Angeles County, and Department of Biology, California State University, Long Beach, California 90840.

³Scientific Officer, Durban Museum, Smith Street, Durban 4001, Republic of South Africa.

accounts include data which are incorrect or which must, after critical study, be attributed to other species. All too often the paucity of original information has led to the same accounts being repeated, summarized, and rephrased so often that even tenuous original observations gain the semblance of well-substantiated facts. Perhaps nowhere is this more true than for the large swifts of the genus *Hirundapus*.

The purpose of this paper is to review the available information on the breeding biology, distribution, and morphology of these swifts as well as to present new interpretations and some new data relating to species limits in the group and the validity of the genus *Hirundapus*. Although neither of us has had any first-hand field experience with any *Hirundapus* swift, both of us have examined museum material of all species and subspecies recognized in this paper. Additionally we have had extensive field experience with a wide variety of other species of swifts. The classification used in this paper is that of Brooke (1970; 1972) although further comments on generic limits in the Apodidae may be forthcoming after completion of studies now in progress (Collins, *in preparation*).

OSTEOLOGY

Studies of the relationships of the swifts have largely dealt with the much debated affinity between swifts and hummingbirds (Trochilidae) (Lowe 1939; Cohn 1968; Sibley and Ahlquist 1972). Only Orr (1963) has used osteological characters in considering the intrafamilial relationships of swifts. He noted substantial variation in the conformation of the transpalatine process within the Apodidae and that in some members of the genus *Cypseloides*, along with *Hemiprocne*, the postero-lateral border of the palatine is angular and not extended into a wing-like transpalatine process as in most swifts. He agrees (personal communication) with our interpretation that in swifts the shape of the transpalatine process is highly diagnostic at the generic level. Swifts of the genus *Chaetura* had the most well-developed and prominent winglike processes to the palatine in each of the three species he examined (Orr 1963: Fig. 3). He did not examine any specimens of *Hirundapus* in his study.

Since that time skeletal material of *H. caudacutus* (2), *H. giganteus* (1), and *H. cochinchinensis* (1) have become available and were examined (by Collins) as a part of this study. Comparative material representing most genera in the Apodidae and six species of new world *Chaetura* were also examined. The transpalatine process in *Hirundapus* is strongly pointed with only a shallow constriction in the lateral edge (Fig. 1; Morioka 1974: Fig. 1). In this respect it is most similar to *Streptoprocne semicollaris* figured by Orr and to the larger species of *Tachymarpis*. There is no similarity at all to the long and usually blunt wings to the palatine, nor the marked constriction in the lateral edge found in *Chaetura* (Fig. 1; Orr 1963: Fig. 3). Also, the prepalatine bar is narrower and concave in *Chaetura* but broader and convex in *Hirundapus*.

No functional significance has been proposed for these observed differences in palatine and transpalatine process. However as pointed out by Morioka (1974) "since the posterolateral edge and transpalatine process provide the points of origin

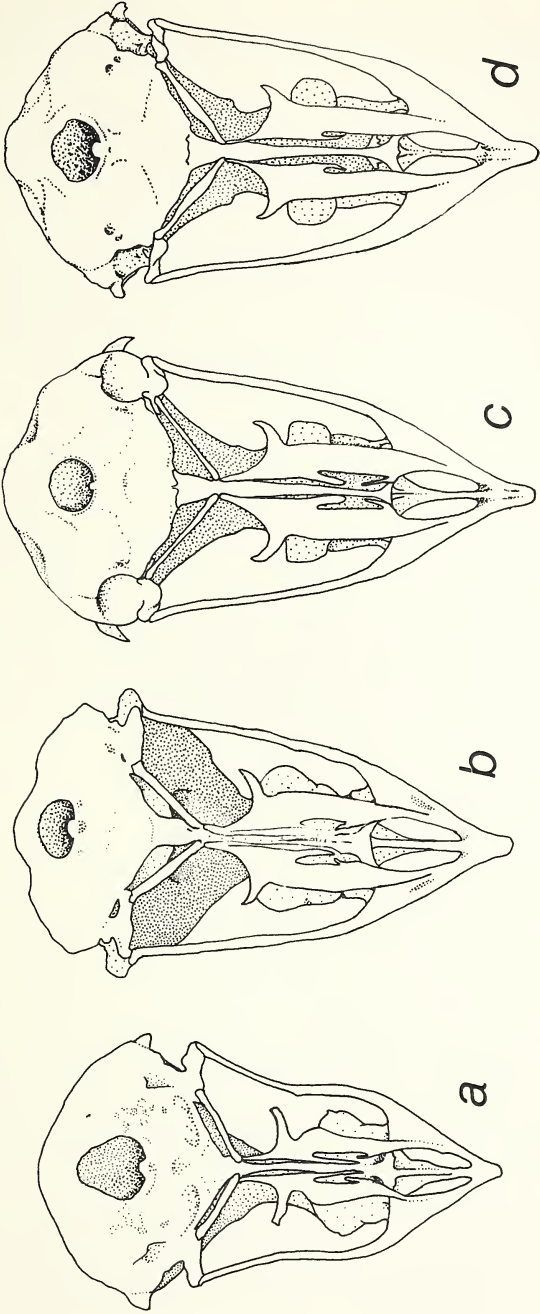


FIGURE 1. Palatine view of swift skulls: a—*Chaetura brachyura*; b—*Hirundapus caudacutus*; c—*H. cochinchinensis*; d—*H. giganteus*. Not to same scale.

for *M. pterygoideus*, one may expect certain variation in the development of this muscle" in those genera of swifts differing in the conformation of the palatine and transpalatine process.

A brief examination of selected postcranial elements of the smaller species of *Chaetura* as well as of more nearly equal-sized species in the genera *Tachymarptis* and *Streptoprocne* indicates that although there is a closer resemblance between *Hirundapus* and *Chaetura* than between these and other genera examined there are numerous differences equivalent to those existing between other distinct genera of the Apodidae. It further appears that these differences are not the result of the differences in body size. We think that these observed osteological differences, particularly those of the palatines, are of sufficient magnitude to support our view of the generic distinctness of *Hirundapus*. These osteological differences will be considered in greater detail at a later date as part of a proposed study of the intrafamilial relationships of the Apodidae based on their osteology.

GENERIC LIMITS

It is our view that excessive weight has been given to the presence or absence of the projecting shafts of the rectrices and inadequate notice has been taken of other highly distinctive, if not unique, characteristics when setting generic limits in spinetailed swifts. The superficial similarity of the tail spines doubtless indicates a certain community of ancestry within the Apodidae, but the number and extent of the differences in plumage, osteology, and breeding biology between *Hirundapus* and *Chaetura*, as well as in their ectoparasites, suggests that this community of ancestry is not recent and does not warrant generic lumping and *Hirundapus* should be given full generic rank within the Apodidae.

THE GENUS *HIRUNDAPUS*

The swifts of the genus *Hirundapus* form a closely knit group of four very similar species which breed from Siberia, Sakhalin Island, and northern Japan south to Taiwan, the Philippine Islands, the Malay peninsula, India, and parts of Indonesia, but not New Guinea. One species, *H. caudacutus*, is highly migratory, wintering in large numbers in parts of eastern Australia and occasionally New Zealand. It has also been recorded as a vagrant in western Europe (Ferguson-Lees 1960; Vaurie 1955). A second species, *H. cochinchinensis*, migrates a shorter distance to wintering grounds in Java and Sumatra (Mees 1973). *Hirundapus giganteus indicus* has been reported as a winter visitor to Malaya (Glenister 1951) while elsewhere this species has been reported to make only more localized seasonal and weather-influenced movements (Jerdon 1862; Whistler and Kinnear 1935; Deignan 1963). This is probably also true of *H. celebensis*.

All of the species in the genus *Hirundapus* are characterized by great size (wings over 170 mm long) and a doubtless well-deserved reputation for being among the fastest flying birds; speeds as high as 170 km per hour have been reported (Gladkov 1942, in Dementiev et al. 1951). The color patterns are largely similar: dark brown

to blackish above and below except for white undertail coverts and in some, lighter or distinctly white throats, and central portion of back paler than the mantle and rump (Fig. 2). These swifts all have a white flank stripe on either side extending upward and forward from the white undertail coverts (Smythies 1968: Pl. 17; Morse and Laigo 1969: Fig. 1; King and Dickinson 1975:204). These white flank stripes are unique within the family Apodidae, although approximated by the white flank patches occurring in *Aeronautes* and *Panyptila*. They have rarely been mentioned in technical diagnoses because most writers were describing museum specimens in which these stripes are largely hidden by the positioning of the folded wings and the legs. White or whitish spots on the inner webs of the tertials occurs in two species, *H. caudacutus* and *H. cochinchinensis* (Fig. 2), and are quite unlike the whitish edges to all the secondaries found in other genera such as *Aeronautes* and *Panyptila*. The presence of dark tips to the undertail coverts in the juvenal plumage of one species of *Hirundapus* is also unique within the Apodidae. A whitish forehead or white loreal spotting occurs in several populations, as discussed below. As reported for *H. caudacutus* (Baker 1927; Ferguson-Lees, 1960) and *H. cochinchinensis* (Mees 1973) as well as other species of swifts (Collins 1968a), the wings of *Hirundapus* swifts have a distinct gloss or iridescence which appears greenish in fresh plumages but soon wears away to a bluish or purple color and eventually to a lusterless dark brown. This is, of course, particularly noticeable in molting birds when very new and very old feathers can be seen side by side.

Anatomically, *Hirundapus* may be characterized as swifts possessing one carotid artery (Garrod 1873), eutaxic wing, well-developed transpalatine process to the palate, anisodactyl feet, rectrices with projecting spineshaped shafts (see below and Fig. 3), no sexual dimorphism in plumage, and the distinctive plumage patterns mentioned above. *Hirundapus* swifts have not been reported as having greatly enlarged salivary glands during the breeding season as reported for many other swifts which use the glue-like secretions of these glands to cement nest material together. These glands have been considered by several authors, the most recent study being that of Naik and Naik (1969). The absence of such glands in *Hirundapus* would not be surprising as it is a group which usually builds no nest; the eggs are laid in a slight depression in the rubbish at the bottom of hollow trees (this will be considered in detail below).

Beddard (1898:226) reported that while *Chaetura spinicauda* has a biceps sling or loop in the leg, *Hirundapus caudacutus* does not. He also reported that *H. caudacutus* alone among the Apodidae examined has a second thigh muscle in addition to the femoro-caudal that is present in all swifts. Further anatomical study may show these characters to be consistent differences between the genera *Chaetura* and *Hirundapus*.

The rectrices of *Hirundapus* swifts possess extremely stiffened shafts which extend well beyond the vane to produce tail spines similar in most respects to those found in *Chaetura*. The rectrices of some of the larger species of *Cypseloides* and *Streptoprocne* are also stiffened but the vane extends to the tip of the shaft (very attenuated in some forms) and the bare spines are the result of the wearing away of the terminal barbs (Orr 1963; Collins, *personal observation*). In *Hirundapus* the tail spines are most weakly developed in *H. caudacutus* and the tail is nearly square. In *H. giganteus* and *H. celebensis*, however, the central rectrices are noticeably longer, producing a

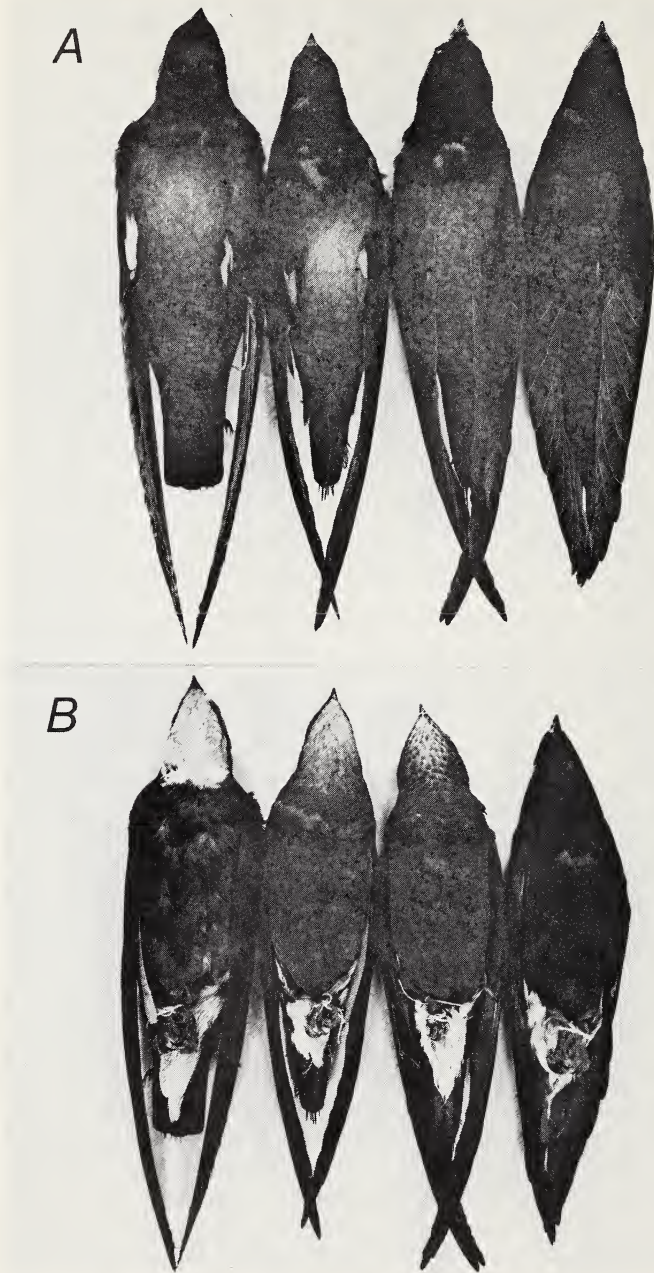


FIGURE 2. Dorsal view (A) and ventral view (B) of *Hirundapus* swifts. Left to right: *H. c. caudacutus*, *H. c. cochinchinensis*, *H. giganteus indicus*, *H. celebensis*.

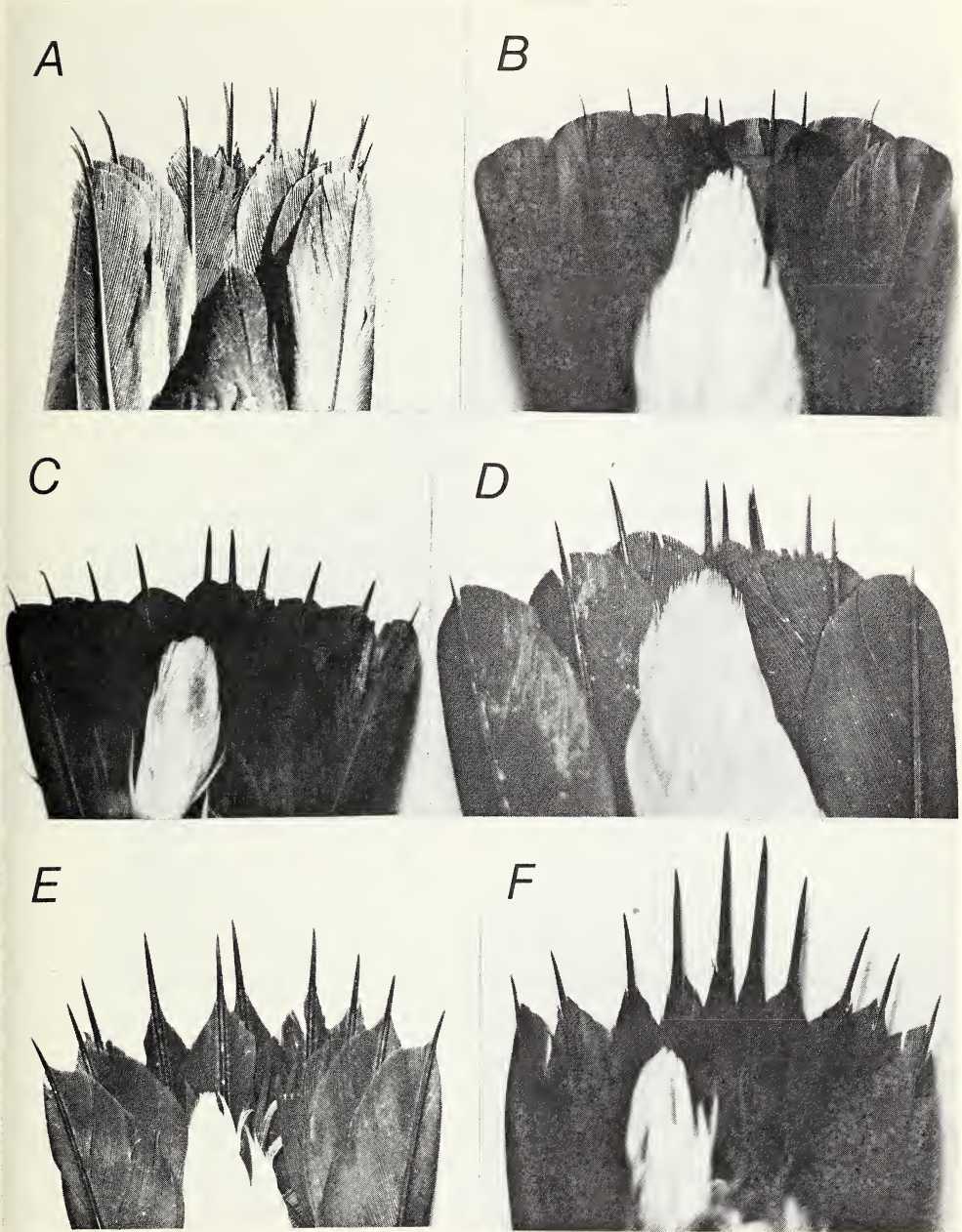


FIGURE 3. Tail spines of *Chaetura* and *Hirundapus* swifts: A—*Chaetura cinereiventris lawrenci*, B—*Hirundapus c. caudacutus*, C—*H. c. cochinchinensis*, D—*H. cochinchinensis formosanus*, E—*H. celebensis*, F—*H. giganteus indicus*. Not to same scale.

more rounded tail (Fig. 3). The shafts of these longer central rectices are also larger in diameter; a condition not unlike that found in many woodpeckers (Picidae). The extent to which this stiffened tail is used by these swifts to support themselves when clinging to the inside of their hollow tree nest sites is presently unknown. Roosting sites are known to include hollow trees, deserted factory chimneys and possibly rocky cliffs (Baker 1927).

The feather lice of the genus *Dennyus* (Mallophaga: Menoponidae) collected from *H. caudacutus* and *H. giganteus* are very different from the lice from other swifts, particularly those from species of *Chaetura*. This has resulted in these lice being placed in the separate subgenus *Takamatsuia* Uchida 1926 (J. A. Ledger, personal communication).

The genus *Hirundapus* was proposed by Hodgson 1836, with the type species *Cypselus nudipes* Hodgson 1836. *Hirundapus* has led a checkered career ever since; it has been accepted and used by some workers in each decade while others have felt it was not sufficiently well-differentiated from *Chaetura* Stephens 1826 with genotype *Hirundo pelagica* Linnaeus 1758 or *Acanthylis* Boie 1826 with genotype *Hirundo spinicauda* Temminck 1810 (Brooke 1974). Lack (1956), the last author before Brooke (1970) to review all genera of swifts, considered *Hirundapus* to be a well-marked group within *Chaetura* but stopped short of giving it generic rank. This view has been followed, largely uncritically, by most recent authors. However, Brooke (1970), reflecting the views presented in this paper, recognized the generic status of *Hirundapus*. We feel that the genus *Pallene* Lesson 1837 with type species *Cypselus giganteus* Temminck 1825 should not be recognized merely because of the lack of white areas in the tertials and stronger purple rather than green iridescence (largely a wear phenomenon, see above) though it might serve as a subgenus.

Until recently the Apodidae has been traditionally divided into two subfamilies, Apodinae and Chaeturinae, on the basis of the number of phalanges in the toes (Sclater 1865), and also the positioning of the toes. Brooke (1970) recognized the New World swifts of the genera *Cypseloides*, *Nephoecetes*, and *Streptoprocne* as being a distinctive subfamily but merged the remaining groups, retaining *Hirundapus* in his Chaeturini within the Apodinae on the basis of its having but one carotid artery. He considered that foot formula did not provide an adequate basis for the subdivision of the Apodidae into Chaeturinae and Apodinae; De Roo (1968) found a typical species of the Apodinae, *Schoutedenapus myoptilus*, to have the unreduced number of phalanges typical of the Chaeturinae.

SPECIES LIMITS IN HIRUNDAPUS

Peters (1940) recognized three species in *Hirundapus*: *H. caudacutus* Latham 1801, *H. giganteus* Temminck 1825, and, provisionally, *H. ernsti* M. Bartels, Jr. 1931. *Hirundapus cochinchinensis* was thought to be "almost certainly a subspecies of *H. c. caudacutus*" and *celebensis* was listed as a subspecies of *giganteus* (Peters 1940:232-233).

Several changes must be made in light of more recent findings. The type of *H. ernsti* has been determined to be a wintering specimen of *H. cochinchinensis* (Mees 1971; 1973) and it is not distinct even at the subspecific level. Full species

status for *cochinchinensis* was advocated by Biswas (1951) who pointed out what he felt to be significant body size and color differences and also cited statements (Baker 1927) that it overlaps the breeding range of *H. caudacutus nudipes* in the hills of northern Burma. In our examination of these species we were impressed by not only the arguments of the earlier workers involving plumage color, body size and presumed breeding range sympatry but also by the appearance of the tail spines. In the case of *cochinchinensis* (Fig. 3) they are intermediate in size between the very reduced spines found in both races of *caudacutus* and the larger spines of *giganteus* and *celebensis*. This difference was independently noted by Mees (1973) in his review of the subspecies of *cochinchinensis*. Although expressing some doubts as to its status, Baker (1927:341) and Peters (1940) retained *cochinchinensis* in *caudacutus* while others (Delacour and Jobouille 1931; Vaurie 1955; Mees 1971, 1973) considered them as separate species, a view which we fully support.

The data presented by Mees (1973) based largely on specimens taken on the wintering grounds strongly suggests that *H. c. cochinchinensis* and *H. c. rupchandi* may be nothing more than ends of a cline in coloration or that the specimens of the lighter colored *H. c. rupchandi* are only extremely worn individuals of the nominate race. Although Mees (1973) now considers *H. cochinchinensis* to be monotypic, we believe *rupchandi* should be recognized at least until more material from breeding areas is available for analysis. Our examination of two recently collected and apparently previously unreported specimens from Taiwan (Yale Peabody Museum #40084 and #40085) confirms our earlier belief that the subspecies described by Yamashina (1936) as *H. caudacutus formosanus* is more correctly included in the species *cochinchinensis*. These Taiwanese specimens agree in color, size, and appearance of the tail spines (Fig. 3) with specimens of *cochinchinensis*, as in fact does the type description, as has been independently noted by Mees (1973). A comparison of these Taiwanese specimens with a series from Java reveals only minor, wear-associated, differences in the color of the gloss (Mees, personal communication). Tentatively we continue to recognize *formosanus*, largely on the basis of its geographic isolation from other populations.

Both *H. giganteus* and *H. celebensis* lack the distinctive white in the tertials found in *H. caudacutus* and *H. cochinchinensis* and have dark throats nearly concolorous with the breast, particularly in *H. celebensis* (Fig. 2). Although stated by Hartert (1892) to be "a very distinct species", *H. celebensis* has been considered conspecific with *giganteus* by most subsequent authors. However, we believe the darker overall coloration, stronger purplish iridescence, and near absence of lighter areas of the throat and back of *celebensis* coupled with a near 40% difference in weight (see below) are significant enough to warrant its being separated from *H. giganteus* and given full species status. The existence of three specimens of *H. celebensis* from Palawan (British Museum [Natural History] *vide* C. W. Benson, *personal communication*) indicates a previously overlooked area of sympatry, *H. giganteus* having been long known from this island (DuPont 1971), and further strengthens our view of the specific distinctness of *H. celebensis*.

A number of subspecies have been proposed in *Hirundapus*, not all of which do we believe are distinct. The presence or absence of a white or pale loreal spot

or forehead as well as differences in the general intensity of the color of the body plumage characterize subspecies in *H. caudacutus* and *H. giganteus*. The subspecific differences in *H. cochinchinensis* are based on color intensity differences only and may be clinal in nature. In *H. celebensis* the subspecific differences characterizing *celebensis*, *dubius*, and *manobo* are strictly mensural and based on a very small number of specimens (Table 1). Awareness of this and the fact that a much greater variation in wing length has been observed in a large sample of *H. caudacutus* (Kleinschmidt 1970) and also in specimens of a similar-sized swift, *Tachymarpis melba* (Brooke 1971b), leads us to believe that *H. celebensis* should be considered as monotypic until a more extensive study can be done based on a more adequate series of specimens. Large numbers of these swifts have been captured in the Philippines by natives protecting their apiaries (see below) but it is doubtful if many have made their way into any museum collection despite the rarity of such specimens.

Several additional specific names have been proposed for *Hirundapus* swifts, and upon re-examination must be placed in synonymy with earlier-named forms. Examination of Stephens (1817:133-134) leads us to believe that his *Hirundo fusca* may well be the same as what has long been known as *Hirundapus c. nudipes* (Hodgson 1836). Stephens (op. cit.) distinguished his *H. fusca* from *H. caudacuta* Latham by *fusca* having a pale dusky brown forehead and *caudacuta* a white one. Hartert (1892:472) acknowledged the presence or absence of a white forehead as the principal difference between *caudacuta* and *nudipes*, which he recognized as separate species, and yet placed *fusca* as a synonym of *caudacuta*. The type locality of *fusca* is not known and according to Hartert (1892:472) the name had not been used since its proposal. On the other hand *nudipes* has a long history of usage in the primary zoological literature, including many of the sources cited in this paper. We therefore consider *Hirundo fusca* Stephens to be an undoubted nomen oblitum and no change of nomenclature is required.

TABLE 1

Wing lengths in millimeters of *Hirundapus celebensis*.

<i>Mindanao and</i>	
<i>Basilian</i>	211, 211, 216, 217
<i>Negros</i>	211, 211, 212, 214, 214, 216, 216, 216, 216, 218, 218
<i>Mindoro</i>	214, 219, 222, 230, 234
<i>Luzon</i>	226, 222
<i>Palawan</i>	190, 192, 194
<i>Celebes</i>	187 ⁴ , 203, 208

Data from: Clarke 1894; Mearns 1905; Rand 1951, Salomonsen 1953; and specimens measured as part of this study: AMNH (Bobbok, Mindoro); Brit. Mus. (Nat. Hist.) (Palawan), fide C. W. Benson, personal communication. Figures for both sexes have been lumped in view of the small size of the samples and the unlikelihood of their being a significant sexual dimorphism in this measurement. Salomonsen (1953) refers the specimens from Luzon and Mindoro to *H. c. dubia* and those from Mindanao, Basilian, and Negros to *H. c. manobo*.

⁴recent fledgling; wing probably not full length.

As noted by Mees (1973) both *H. klaesii* Buttikoffer 1887 from Sumatra and *H. ernsti* (M. Bartels, Jr. 1931) from Java are attributable to *H. c. cochinchinensis*. The type description of *H. caudacutus bourreti* (David-Beaulieu 1944) as well as a re-examination of the type, collected at Xieng-Khouang, Laos, leaves no doubt that it is correctly referable to *H. c. caudacutus* (Dickinson 1970). Little is known of the exact route taken by *H. c. caudacutus* when migrating from wintering grounds in Australia to northern breeding grounds in parts of Siberia. They are known to reach some parts of their breeding grounds as late as the second half of May or early June (Neufeldt and Ivanov 1960) at which time some are still en route in southernmost areas of China (Dementiev et al. 1951). The date of collection of *bourreti* (24 April 1940; David-Beaulieu 1944) is consistent with its being considered a migrant individual of *H. c. caudacutus* and not part of a resident population. *Hirundo sinensis* Gmelin (1789) seems more likely to refer to a swift than a swallow as has been commonly assumed. It may well refer to *H. caudacutus*, the only member of this taxon to occur in China, but the errors in the description make it indeterminate and it must be considered a nomen dubium. Our view of the genus and its forms can be summarized as follows:

GENUS *Hirundapus* HODGSON

Hirundapus Hodgson 1836, Jour. As. Soc. Bengal, 5:780. Type, by original designation and monotypy, *Cypselus nudipes* Hodgson.

Pallene Lesson 1837, Compl. Buffon, 8:493. Type, by monotypy *Cypselus giganteus* Temminck.

HIRUNDAPUS CAUDACUTUS

Hirundapus caudacutus caudacutus (Latham)

Hirundo caudacuta Latham 1801, Index Orn., Suppl. p. Ivii.—New South Wales, Australia.

Hirundo ciris Pallas 1811, Zoogr. Rosso-As., 1:541.—Siberia.

Chaetura australis Stephens 1826, Gen. Zool., 13:76—New South Wales, Australia.

Chaetura macroptera Swainson 1833, Zool., Ill., pl. 42—type locality unknown.

Chaetura caudacuta bourreti David-Beaulieu 1944, Publ. Univ. Indochina, p. 89—Xieng-Khouang, Laos.

Breeds in Siberia, northern China, Sakhalin, and Japan. Migrates through eastern China and Laos, winters in Australia, Tasmania, and rarely New Zealand. Accidental in Europe.

Hirundapus caudacutus nudipes (Hodgson)

Cypselus nudipes Hodgson 1836, Jour. As. Soc. Bengal, 5:779—Nepal.

Hirundo fusca Stephens 1817, Gen. Zool., 10:133—type locality unknown. (Stephens, op. cit.: 134)

Cypselus leuconotus Delessert 1840, Mag. Zool., pl. 20—Bhutan.

Breeds in northeastern Pakistan and Himalayas south and east to Assam and southwestern China.

HIRUNDAPUS COCHINCHINENSIS

Hirundapus cochinchinensis cochinchinensis (Oustalet)

Chaetura cochinchinensis Oustalet 1878, Bull. Soc. Philomath. Paris, 2:52—Saigon, Vietnam.

Hirundapus klaesii Buttkofer 1887, Notes Leyden Mus., 9:40—Sumatra.

Chaetura ernsti M. Bartels, Jr. 1931, Orn. Monatsbr., p. 54—Haliomen Mountains, Java, Indonesia.

Breeds in Assam in India, eastern Thailand, and Indochina. Winters in Sumatra and Java.

Hirundapus cochinchinensis formosanus (Yamashina)

Chaetura caudacuta formosana Yamashina 1936, Orn. Monatsbr., 44:90—Arisan, Taiwan. Island of Taiwan.

Hirundapus cochinchinensis rupchandi (Biswas)

Chaetura cochinchinensis rupchandi Biswas 1951, Ardea, 39:320—Hitaura, Neapl.

Nepal (presumably breeding). Winters in Java and Sumatra.

HIRUNDAPUS GIGANTEUS

Hirundapus giganteus giganteus (Temminck)

Cypselus giganteus Temminck 1825, Pl. col., livr., 61, pl. 364—Bantam, Java.

Breeds in Malaya, Sumatra, Java, Borneo, and the Palawan Island group of the Philippines.

Hirundapus giganteus indicus (Hume)

Chaetura indica Hume 1873, Stray Feath., 1:471—Andaman Islands.

Breeds in India, Bangladesh, Ceylon, Andaman Islands, Burma, Thailand, and Vietnam.

HIRUNDAPUS CELEBENSIS

Hirundapus celebensis (Sclater).

Chaetura gigantea var. *celebensis* Sclater 1865, Proc. Zool. Soc. Lond., p. 608—Menado, Celebes, Indonesia.

Chaetura dubia McGregor 1905), Bureau Govt. Labs., Manila, 34:15—Mindoro, Philippines.

Chaetura gigantea manobo Salomonsen 1953, Vidensk. Medd. Dansk. Naturh. Foren., 115:239—Malaybalay, Bukidnon Prov., Central Mindanao, Philippines.

Occurs (presumably breeding) in Celebes, and Philippines including Palawan Island group.

The order of species presented here assumes the increasing specialization of the tail spines to be the most important phylogenetic trend in the genus. If however, increasingly patterned and colored plumage were held to be the most important trend the sequence might be nearly the reverse. This matter cannot be considered further until a phylogenetic analysis of the Apodidae has been undertaken.

AGE ASSOCIATED DIFFERENCES IN PLUMAGE

Although no sexual differences in plumage have been detected in any *Hirundapus* species, some age associated differences have been recorded. The juvenal plumage of *H. caudacutus*, as mentioned earlier, has dark tips to the white under-tail coverts. This species is also noted as having the ends of the "white lower wing coverts spotted with black-brown markings" (Dementiev et al. 1951), a feature we have not been able to confirm as these coverts are all uniform brown in the specimens of *H. caudacutus*, *H. cochinchinensis*, and *H. giganteus* we have examined. Comment has also been made that in juvenal plumaged birds the white forehead of *H. caudacutus* and the white loreal spots in *H. giganteus indicus* are less extensive,

or dusky or "mouse colored" (Dementiev et al. 1951; Abdulai 1964), characters we have been unable to confirm in this study. One specimen of *H. celebensis* (USNM 247744) has distinctly brownish loreal spots and may well be the basis for the statement by Salomonsen (1953:240) that this race has the "loreal spot sooty grey (possibly due to staining)". However, two syntypes of *H. celebensis* have "pure white and very conspicuous" loreal spots (G. F. Mees, *personal communication*). Closer examination of the brown lored specimen, a male, shows it to be in very fresh unworn plumage with all of the primaries ensheathed at the base, a condition which can only be found in a nestling or recently fledged juvenal plumaged bird; adults would only have one or two primaries in molt at one time. The undertail coverts of this specimen are white and lack the dark tips of juvenals of *H. caudacutus*. The loreal spot is dusky or brownish in color and since this color includes the full length of the loreal feathers and not just the tips it is unlikely to be the result of staining. The edges of the underwing secondary coverts in this specimen are broadly dusky grey-brown and not whitish as true in adult specimens. Meyer and Wigglesworth (1898) also report brown lores for a "♀ juv." specimen thus making it clear that this condition represents an unreported juvenal plumage character of *H. celebensis*, not shared with *H. giganteus*, rather than a racial character or sexual dimorphism in plumage, the latter being uncommon in swifts and otherwise unknown in *Hirundapus*. Further study is needed before a juvenal plumage can be characterized for *H. giganteus* and *H. cochinchinensis*.

BODY WEIGHTS

Information on body weight in *Hirundapus* swifts is scarce. Neufeldt and Ivanov (1960) present data for *H. c. caudacutus* obtained from specimen labels in the Leningrad Museum; 11 males ranged from 109 to 140 gm (average 122.2) while 5 females ranged from 101 to 125 gm (average 113.7). The male type of *H. c. nudipes* weighed 4½ oz (± 127 gm) (Hodgson 1836). In Thailand, body weights of two males of *H. giganteus indicus* were 134.0 and 124.5 gm and an unsexed specimen weighed 123.0 gm while a third male of this species which was "very fat" was appreciably heavier (167.0 gm) (J. T. Marshall, *personal communication*). Body weights for a male and an unsexed specimen of *H. c. cochinchinensis* also from Thailand were respectively 76.1 and 85.5 gm (J. T. Marshall, *personal communication*). It is interesting to note that although *H. cochinchinensis* is only slightly shorter winged than *H. caudacutus* it appears to be significantly lighter in weight. If this is borne out by additional data it would imply an appreciably different wing loading for this species and perhaps equally different foraging procedures, enhancing its capacity to maintain syntopy with its heavier congeners which sometimes forage with it in the same flock (Delacour and Jabouille 1931:288). The data presented by Morse and Laigo (1969) for *Chaetura dubia* (= *H. celebensis*) in the Philippines indicate that it ranges in weight from 170 to 203 gm (22 unsexed specimens; 2—27 February 1968) and averages 179.6 grams. From these limited data it appears that on an average *H. celebensis* is possibly as much as 40 per cent heavier than *H. giganteus* with all recorded individuals of *H. celebensis* being heavier than

even the heaviest *H. giganteus*. These data further support the specific distinctness of *H. celebensis*. In summary, *Hirundapus caudacutus* weighs 101-140, *H. cochinchinensis* 76-86, *H. giganteus* 123-167, and *H. celebensis* 170-203 grams.

The apparent sexual dimorphism in body weight in *H. caudacutus* may only be due to the size of the samples used and may not be significant. The available data for some larger African species of *Apus* show near equality in body weight with the heaviest birds being individual females (Brooke 1969). A slight but significant sexual dimorphism in body weight has been shown for two small neotropical species, *Cypseloides rutilus* and *Aeronautes montivagus*, with males being heavier than females in both cases (Collins 1968b, 1972).

NESTS AND NEST SITES

Lack (1956) has shown that in the Apodidae, genera are usually characterized by distinctive nesting habits and, frequently, clutch sizes. There is no reason to doubt the application of this observation in *Hirundapus*. A number of nests have been found in a wide variety of locations and attributed to members of this genus. Few of these were authenticated by specimens or other satisfactory evidence. In some cases the assumed attribution seems to have been based on little more than the observation of *Hirundapus* swifts in an area where unidentified nests were found.

In one of the earliest accounts (Baker 1897), nests attributed to *H. giganteus indicus* were found on the walls of dark cavelike passages in deserted lime quarries in North Cachar, Assam, India. The nests were masses of mossy plant material and bear hair collected from an adjacent bedding area of the bears and held together with mud; later accounts of these same nests also mention the use of saliva in the nests (Baker 1927; 1934). Adult swifts were seen nearby and were flushed from the nest area but none appear to have been collected. One of the three nests, however, contained three nearly fledged young which showed the tail spines and white loreal spot of the adults. In a later account, however, these nests are re-attributed to *H. cochinchinensis* (Baker 1927); a change which is not clearly explained or consistent with the previous description of the young as having a white loreal spot. Such a spot is present in *H. giganteus* but lacking in *H. cochinchinensis*! and in still another account Baker (1934) expresses the opinion that the nests were more likely to be those of *Micropus subfurcatus* (= *Apus affinis nipalensis*) and that the *Hirundapus* swifts had taken over the nests of the smaller species. Even so, the description of the nests is unlike those of *A. affinis* anywhere in its range but is typical of cave swiftlets of which only one, *Aerodramus brevirostris* breeds in the area (Ali and Ripley 1970). Baker (1934) also expresses the view that:

it is probable that the above instance of Spinetails breeding in a cave may be exceptional, as I never got others, though we worked very hard for them. The whole of this country for miles upon miles was open park-land dotted over with great black Oaks, a very large percentage of which were hollow, so it seems more probable that such trees formed the normal breeding places for the Spinetails.

Unfortunately Baker's later reassessments as to the actual builders of these nests and the unusual, if not unique, positioning of these nests have not been incorporated

by subsequent authors. This has led to paraphrased accounts of the earlier conclusions being repeated widely even in recent literature, and a rocky cliff nest site with a nest of moss and saliva being considered typical of *H. cochinchinensis* and distinctive within the genus. What may have happened is that *H. giganteus* used a pre-existing nest of *A. brevirostris*, an atypical if not unique situation.

The best account of breeding in *Hirundapus*, accompanied by photographs of the nest site, is that by Neufeldt and Ivanov (1960) summarizing the information of Gizenko (1955) and Lobko-Lobanovski (1956), for *H. caudacutus* in Siberia and on Sakhalin Island. Its fullness of data and the care for identification with which it was obtained warrant taking this information as the standard of comparison for additional nesting records of *Hirundapus* swifts. Jahn (1942) and Austin and Kuroda (1953) show that there is no significant difference in the breeding of this species in Japan. The basic feature of these accounts is that nests are mere depressions or scrapes in the rubbish and detritus in the bottom of large hollow trees. These authors found no evidence that these large swifts bring any nest material to the site; they simply scrape or utilize a shallow depression in the nest site substrate, as is also true of the largest new world species, *Streptoprocne semicollaris*, which lays eggs on bare sandy ledges in caves (Rowley and Orr 1962).

Baker (1934) describes similar nests and nest sites for *H. giganteus indicus* on the basis of observations provided by J. Stewart who apparently examined numerous such sites, including eggs as well as young and adults captured in the hollow trees. Baker (1934:466) states that "although the birds roost in hollow trees in quite big flocks, only one, rarely two, or at the outside three, pairs will breed in the same tree." In an earlier account that he himself published Stewart (1913) describes in greater detail the finding of three nest scrapes in the bottom of one tree, *only one of which contained eggs or young!* He also mentions finding in another tree, two nests each of which contained two fresh eggs. No other account of *Hirundapus* breeding mentions the use of a single hollow tree by more than one pair at one time. By their own admission (Stewart 1917; Baker, 1934) the presence of more than one active nest per tree is very unusual. It is distinctly probable that both theirs and all subsequent references in the literature to this day of more than one pair breeding in the same tree are based on these two incidents. It is quite possible that the additional scrapes observed in the first incident represented nest scrapes of previous years or trial scrapes made early in the present nesting season and that only one was active at the time. It is also possible that the one recorded case of two sets of two eggs in a single tree could represent a more normal clutch of four accidentally divided between two scrapes. Such accidental occurrences are not unusual in birds. It is very doubtful that there are any valid records of two pairs ever nesting in the same tree at the same time. The suggestion that three nests per tree is possible, attributed to Stewart by Baker (1934; see quote above) is almost certainly based on the single incident mentioned above and is not consistent with the previously published statement that he had "not found more than *two* pairs breeding in one tree" (Stewart, 1913). The inconsistencies in these various accounts are compounded by the feeling stated by Ali (1953:13) that some of the notes and discoveries by Stewart as reported by Baker were "unfortunately of not unimpeachable authenticity."

Stewart (1913) also mentions that the nest scrapes of *Hirundapus giganteus indicus* were "lined with dry leaves and straw", a feature not noted in any other account of *Hirundapus* nests. However, there has been one recorded observation of this species "flying with a straw in its mouth" (Bourdillon, *in* Fergusson 1904: 661) during the suspected breeding season.

Allen (1960) reported a nest of *H. g. giganteus* found on a ledge behind a waterfall in Malaya. The similarity of this nest and eggs to those of *Hydrochous gigas*, another large swift of that part of Malaya, was independently noted by ourselves in this study and Somadikarta (1968). This view has been confirmed by Becking (1971) who examined feathers adhering to the brim of this nest, glued there by saliva used in nest construction.

The nests of *H. celebensis*, as well as those of other races of the other three species of *Hirundapus* remain undescribed. The suggestion that *H. celebensis* "builds its nests in caves" on the Island of Negros in the Philippines (Clarke 1898) is based on information gained from natives by his collector. Such hearsay evidence from natives who, in our experience, frequently do not differentiate between the several species of swifts present in an area, is extremely uncertain. Thus this suggested sea-cave nest site is considered by us to be an unlikely possibility both in the light of the amount of well-documented information presented above for other species and the distinct possibility that they were referring to a cave nesting species of the Collocaliini and not a member of the genus *Hirundapus*. Jerdon (1862) was led to search sea caves and cliffs for nests or roosts of *H. g. indicus* with no success at all.

Despite the prevalence of information in *original sources* supporting hollow tree nest sites for *Hirundapus* swifts most recent works considering these swifts continue to mention rocky cliff nesting and/or roosting sites. The original sources for these statements are usually not mentioned and in some cases appear to be based on the atypical nesting situation of *H. g. indicus* discussed at length above. Colonial nesting in steep rocky banks is reported for *H. caudacutus* (Johansen 1915; *in* Dementiev, et al 1951). The same species is also reported to roost in great numbers on the vertical faces of limestone cliffs (Baker 1927:342) or in "hollows or cracks in the rocks" (Dementiev, et al 1951). In both of these cases no details were presented to substantiate this and we believe they should be questioned and may well be based on observations of other species of swifts. The account of LeSouef (1907) of *H. caudacutus* nesting on ledges near a waterfall in Japan is accompanied by detailed observations but no specimen was collected. However, as mentioned above, other accounts of the nesting of *H. caudacutus* in Japan are in agreement with a hollow tree nesting site and thus the observations of LeSouef are certainly atypical if correctly attributable to this species.

Although it is not yet possible to exorcise from the literature the numerous general accounts of rocky cliff nesting and roosting sites for *Hirundapus* swifts, it is hoped that all future authors dealing with this point will carefully examine the arguments presented here and also the few original sources available and not simply repeat what others have said and thus perpetuate the uncritical and frequently erroneous accounts of their predecessors.

We are strongly of the opinion that descriptions of rocky cliff nesting and roosting sites for *Hirundapus* swifts are atypical at best, and frequently erroneous. We do not agree with recent statements such as that by Harber (1955) that "nesting in cliffs has been disputed but is now established for certain localities."

EGGS AND CLUTCH SIZE

The eggs of *Hirundapus* swifts, like those of nearly all other swifts, are pure porcelain white but frequently become discolored during incubation. The average dimension of 28 eggs of *H. c. caudacutus* from Sakhalin Island were 32.27×22.34 mm (Neufeldt and Ivanov 1960) while a single egg removed from the oviduct of *H. caudacutus nudipes* measured 31.2×22.4 mm (Baker 1927). Eggs of *H. c. caudacutus* from Japan (Austin and Kuroda 1953) are similar in length (27.5 to 31.2 mm) but appear to be somewhat smaller in width (17.5 to 19.3 mm). A single egg from the oviduct of *H. c. cochinchinensis* measured 28.1×21.0 mm while a sample of 100 eggs of *H. giganteus indicus* averaged 29.6×22.2 mm; maxima 32.1×22.5 and 31.2×23.5 mm; minima 28.8×22.0 and 29.9×20.0 mm (Baker 1927). Nine fresh eggs of *H. c. caudacutus* weighed between 7.95 and 8.93 grams (Neufeldt and Ivanov 1960).

The clutch size in *Hirundapus* ranges from two to seven eggs and incubation, in *H. caudacutus* at least, is said to start with the first egg (Neufeldt and Ivanov 1960). This is a common feature in the reproductive strategy of raptors for which the ease of finding food for the young varies greatly in different years, but an adaptation otherwise unknown in the Apodidae.

BEHAVIOR

Observations of display behavior of swifts are fragmentary and generally hampered by the extreme mobility of these birds and the resultant short periods of continuous observation. On its wintering grounds in Australia, several apparent displays by *H. caudacutus* have been recorded and which appear to be unique in the family. On several occasions individuals have been noted to "tumble," "dive," or "gravity drop" from a flock circling high over head (Simpson and Noonan 1967; d'Ombraïn 1934). After vertical drops of from six to nine meters up to 30 m or more the birds quickly rose to join the circling flock. Although several members of the flock were engaged in these activities, repeated performances by more than one of these individuals were recorded. The significance of this activity is not understood but a sexual display function is suggested (Simpson and Noonan 1967) though this seems unusual for birds in winter quarters. Steep dives at high speed to nearly ground level have also been recorded as part of feeding activities (Cameron 1968) on the wintering grounds and similar dives have been observed on the breeding grounds by Gladkov (1942; in Dementiev et al. 1951).

Flocks of both *H. caudacutus* and *H. giganteus* feeding over water have been observed to fly low over the surface in a tight circle, with individuals occasionally dipping down to drink or possibly bathe (D'Ombraïn 1934; Cameron 1968; Smythies

1968; Ali and Ripley 1970:37). Drinking and bathing on the wing in a similar fashion have been observed for single individuals, but not flocks, of *Chaetura pelagica* (Vaurie 1947) and for several other species of New World and Ethiopian swifts (Collins, *personal observation*; Brooke 1973). Such activities are apparently risky maneuvers as on two occasions, both in Australia, individuals of *H. caudacutus* have been seen to crash into the water (Cameron 1968; G. Bennett, *personal communication*) possibly from having inserted the mandible too deeply in the water when flying at such high speeds. In both cases the birds did not swim and were not successful in rising from the water but flew away strongly when thrown aloft. Wounded individuals of *Tachymarpis melba africanus* and *Apus b. bradfieldi* which fell in the water were observed to swim strongly with their wings outstretched (Brooke, *personal observation*).

Smythies (1953:365) also reports that in Burma *H. giganteus* can be heard to make a distinct drumming sound while drinking "not unlike the drumming of a snipe" and "when rising from the water the wings are brought together over the back with an audible smack". Ali and Ripley (1970:36) state that "the wings (of *H. giganteus*) produce a loud twanging sound (as of a harp string) as the birds hurtle past overhead". Such noise-making is uncommon among swifts. Bednall (1963) records a similar "drumming" noise made by a spreading and twisting of the tail at the start of a dive by *Tachymarpis aequatorialis*. Several *Chaetura* species make wing-clapping noises as a threat display at roosts but not in flight (Collins 1968a, 1968b).

The vocalizations of *Hirundapus* swifts as described by numerous authors include a loud squeaking or screaming cry uttered in flight and also a sharp clear note. It is presumably the latter vocalization that is referred to in Smythies (1968) as a "harsh loud call like a magnified flowerpecker".

In *Apus apus*, nonbreeding birds ascend high in the air, sometimes over the sea, at dusk, and remain on the wing all night. This has been discussed by numerous authors and most recently reviewed by Eastwood (1968) and Lockley (1971). This also has been observed for *Streptoprocne zonaris* in Trinidad (Snow 1962; Collins, *personal observation*) and been attributed to all old world swifts away from their breeding grounds by Brooke (1971a). It appears that this also occurs in *H. giganteus indicus*: Jerdon (1862) observed an enormous flock, presumably of non local breeding birds, heading out to sea at dusk on the Malabar coast of India. He made a search for a roost and/or breeding site along the coastal cliffs and an offshore islet but without success.

FOOD

The diet of *Hirundapus* swifts has not been studied in detail although some food items, all insects, have been listed for each of the four species. The orders and families of insects involved include: Ephemeroptera, Orthoptera, Hemiptera, Odonata, Diptera (Phoridae), Coleoptera (Scolytidae, Coccinellidae), Hymenoptera (Vespididae, Formicidae, Apidae, Ichneumonidae, Bombidae).

In the Philippines, *H. celebensis* has become an important predator of the workers and drones of honey bees (3 species of *Apis*) (Morse and Laigo 1969). The swifts are collected in large numbers by the natives when they are flying low over fields near the apiaries; approximately 450 were so captured between January and March 1968. Bee eating has also been recorded for *Tachymarpis aequatorialis* (Brooke 1973) in Africa and may be common among swifts.

Although on occasion they forage near ground level or over water, *Hirundapus* swifts usually forage high above the ground, frequently utilizing updrafts associated with cliffs and escarpments. It is probably this latter habit that has so often and, we believe erroneously, led to their being associated with these cliffs for nesting and roosting as is the case with some more familiar swifts, particularly those of the genus *Apus*.

ENGLISH NAMES

Despite the objections which can be raised we consider that "needletail" would make the best group name; it has only been used for members of this genus and it does draw attention to the remarkably long, large projecting shafts of the rectrices. This recommendation has been recently adopted by King and Dickinson (1975). As for the species names, White-throated and Brown-throated have long been in use, particularly in India, and are also diagnostic species characters as shown above. King and Dickinson (1975) however, use White-throated, Brown, and White-vented for the three species they consider. The literature does not provide a suitable name for *H. celebensis* which we propose to call the Purple Needletail. In short:

White-throated Needletail	<i>H. caudacutus</i>
White-vented Needletail	<i>H. cochinchinensis</i>
Brown-throated Needletail	<i>H. giganteus</i>
Purple Needletail	<i>H. celebensis</i>

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INSECTIVORA AND PROTEUTHERIA OF THE LATER EOCENE
(UINTAN) OF SAN DIEGO COUNTY, CALIFORNIA

By MICHAEL J. NOVACEK

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INSECTIVORA AND PROTEUTHERIA OF THE LATER EOCENE (UINTAN) OF SAN DIEGO COUNTY, CALIFORNIA¹

By MICHAEL J. NOVACEK²

ABSTRACT: A highly diverse fauna of Insectivora and Proteutheria (Mammalia) from Uintan strata (later Eocene) of San Diego County, California, includes at least twelve species representative of a minimum of six families. *Sespedectes singularis*, an adapisoricid erinaceoid, is the most abundantly represented species. *Proterixoides*, a genus closely related to *Sespedectes*, is extremely rare in San Diego localities. A new genus and species, *Cryptolestes vaughni*, is intermediate in some aspects of dental morphology between *Sespedectes* and *Proterixoides* and certain other adapisoricids. *Batodonoides powayensis*, another new genus and species allocated to the Geolabididae, shows strong similarities with *Batodon tenuis* and *Centetodon* spp. The local fauna suggests the presence of a primitive apternodontine and a palaeoryctine. Also present is an aberrant new genus and species, *Aethomylos simplicidens*. There are strong indications of endemism in the San Diego insectivore fauna. Of the 12 taxa described, only *Apatemys*, *Nyctitherium*, and *Centetodon* are known elsewhere in North America. The local insectivores seem generally more primitive than those of later Eocene faunas from the midcontinent of North America.

INTRODUCTION

The later Eocene (Uintan) terrestrial vertebrate fauna of San Diego County was first studied by Dr. Chester Stock (1937, 1938, 1939). Since the time of Stock's early work, little research on this fauna has been published (see Lillegraven 1973, for a summary of previous work). Such a dearth of literature is a reflection of neither the scarcity nor the insignificance of San Diego Eocene vertebrates. Southern California Uintan terrestrial deposits, which include both strata from the greater San Diego area and the Sespe area north of Los Angeles, are widely separated geographically from all other North American vertebrate fossil bearing deposits of this age. Therefore, the southern California faunas are significant because they represent a later Eocene biogeographic region far removed from midcontinental regions. Furthermore, San Diego Uintan nonmarine beds are in close proximity and, in some cases, even inter-tongue with marine strata, allowing for chronostratigraphic correlation between marine and nonmarine fossils (see Black and Dawson 1966; Lillegraven 1973, for further discussion).

This report is an early contribution to a long-term project concerned with the salvage and study of later Eocene fossil vertebrates from the San Diego region. It i

¹REVIEW COMMITTEE FOR THIS CONTRIBUTION:

DAVID J. GOLZ
JASON LILLEGRAVEN
DONALD E. SAVAGE
DAVID P. WHISTLER

²University of California Museum of Paleontology, Berkeley, California 94720.

primarily a systematic work and deals with only one aspect of the local vertebrate fauna, the Insectivora (and Proteutheria). Hitherto, only three studies have been published on Eocene insectivores from southern California. Stock (1935) described and named two erinaceid-like insectivores, *Sespedectes singularis* and *Proterixoides davisii* from the Sespe Formation, a unit of late Eocene age located in Ventura County, north of Los Angeles. In the same publication, Stock briefly described a possible leptictid species represented by a lower jaw fragment with a third molar. Gazin (1958) named a new apatemyid species, *Apatemys downsi*, from the Sespe collections. Most recently, Coombs (1971) described *Simidectes*, an insectivore known from the Sespe Formation. Although *Simidectes* is also represented in the "Laguna Riviera" faunal collections made by the University of California Museum of Paleontology (Coombs 1971:18), this genus has not yet been discovered in any Uintan locality in the greater San Diego area.

Not all of the insectivore species represented in the San Diego Uintan collections are described in this paper. Some of the geolabidines recovered will be discussed in a forthcoming review of the Geolabidinae by Lillegraven and McKenna (MS.). There are several specimens referable to *Uintasorex* or a closely related genus. *Uintasorex* has recently been recognized as a member of the Microsyopidae by Szalay (1969b), a family which is periodically shifted in its allocation between primates and insectivores (see Szalay 1969a, 1969b, 1971). A thorough consideration of the San Diego *Uintasorex* species has been completed by Lillegraven (In Press). The San Diego genera *Sespedectes* and *Proterixoides* are described in a review of later Eocene erinaceoid insectivores of southern California (MS.).

LOCALITIES

The marine, nonmarine Eocene section in the San Diego area was recently redefined by Kennedy and Moore (1971) who raised the original Eocene Poway Conglomerate to group status. They further subdivided this unit into the basal Stadium Conglomerate, the Mission Valley Formation, and an unnamed formation above the Mission Valley. Occurring stratigraphically below the Stadium Conglomerate is the chiefly nonmarine Friars Formation, the uppermost unit of the La Jolla Group. Uintan vertebrate fossils have been collected from about sixty localities within the Friars Formation, Stadium Conglomerate, and Mission Valley Formation. Detailed descriptions of these localities are on file at the University of California, Berkeley, Museum of Paleontology.

One locality, V-72088, at the northern end of the Camp Pendleton Marine Corps Base near Camp San Onofre, has yielded a significant sample of small vertebrates, including insectivores. The specific stratigraphic position of V-72088 is currently unknown, but the mammalian fauna is Uintan and appears to correspond closely with that of the Mission Valley Formation.

Table 1 summarizes the current distribution of insectivore taxa by locality. Neighboring localities in the same formation are grouped together under "local areas" which correspond to those designated on the map (Fig. 1). It is evident that

many taxa are poorly represented, in some instances by only one or two isolated teeth or fragmentary jaws. An exception is observed in the case of *Sespedectes singularis*. Fossils representing this species are abundant and widely distributed. The lower molars of the second most abundant species, *Cryptolestes vaughni*, when severely worn are indistinguishable from those of *Sespedectes singularis*. Consequently, where only lower molars were found, they could not be assigned with great assurance to either species. This is denoted in the table by equal fractions in parentheses put in rows opposite both *S. singularis* and *C. vaughni*. At certain other localities, it was arbitrarily decided that if only diagnostic teeth of one species were found, all specimens including lower molars were referred to that one species. The lack of verification for such an action is signified in Table 1 by question marks preceding the fraction.

While a large sample (243 + specimens) referable to *Sespedectes singularis* has been recovered from locality V-72088, the only other insectivore species known from the locality is *Proterixoides davisi*. A strikingly different insectivore assemblage is represented at locality V-72158. Both *S. singularis* and *P. davisi* are absent, but a closely related species, *Cryptolestes vaughni*, is represented by a large number of specimens (68 +). Even more interesting is the fact that eight different insectivore taxa are represented at V-72158. This difference seems to be consistent throughout the localities listed in Table 1, but only at V-72088 and V-72158 are samples large enough to clearly illustrate the pattern.

The simplest interpretation for the faunal differences between V-72088 and V-72158 is that these localities represent distinctly different microhabitats. Collecting bias is probably a minimal factor as quite large samples of matrix from both localities were washed and sorted for microfossils. The fossiliferous unit from V-72088 is a rather coarse, poorly indurated sandstone. Clayballs present in the unit are rounded or spherical, suggesting that they were transported some distance by water currents. The fossiliferous matrix at V-72158 is predominantly a green silty claystone with minor amounts of sand. These differences suggest that fossils were deposited under relatively higher energy conditions at V-72088 than at V-72158.

It is interesting to note that although V-72088 seems to represent a relatively higher energy depositional environment, insectivore fossils preserved in that locality were less fragmentary than those preserved in V-72158. Twenty-eight mandibles with two or more teeth of *S. singularis* were recovered at V-72088. At V-72158, in contrast, insectivores were mainly represented by isolated teeth or edentulous jaw fragments. Voorhies (1969:22) suggested that the ratio of upper dentitions to lower dentitions of small mammals is inversely related to a greater current energy because maxillae of large and small mammals tend to break up and lose their teeth more readily than mandibles. This generalization is supported by the observation that only three maxillae of *S. singularis* were recovered from V-72088 in comparison to the twenty-eight mandibles recovered. When the total number of teeth both in and out of jaws is counted, the percentage of uppers to lowers is 53%. The ratio of the upper to lower dentitions from V-72158 referable to *Cryptolestes vaughni*, a species nearly the same size as *S. singularis*, is 74%. There might be an explanation to account for both this difference in percentages and the greater number of preserved lower jaws

TABLE I
Distribution of taxa by locality

	UNNAMED FORMATION		MISSION VALLEY FORMATION				
	San Onofre Locality		Poway Localities		Fletcher Hills Localities		
Species ³	V-72088	V-71180 V-71181 V-71211 V-72157 V-72158 V-72176 LACM	65190	V-6871	V-6893	V-71055	
cf. <i>Apatemys</i> sp.			$\frac{1}{2}$				
? <i>Palaeoryctine</i> gen. and sp.							
<i>Sespedectes singularis</i>	$\frac{32}{243}$				$\frac{3}{3}$	$\frac{2}{15}$	$\frac{3}{23}$
cf. <i>Proterixoides davisi</i>	$\frac{1}{4}$						$\frac{2}{3}$
<i>Cryptolestes vaughni</i>	$\frac{2}{7}$	$\frac{1}{1}$	$\frac{2}{10}$	$\frac{6}{68}$	$\frac{1}{1}$		
cf. <i>Nyctitherium</i> sp.	$\frac{1}{1}$			$\frac{1}{1}$			
<i>Centetodon</i> spp.	$\frac{1}{1}$		$\frac{2}{5}$	$\frac{2}{16}$			
<i>Batodonoides powayensis</i>		$\frac{1}{1}$	$\frac{2}{7}$	$\frac{1}{1}$			
? <i>Apternodontine</i> gen. and sp.							$\frac{1}{1}$
Erinaceoid-like gen. and sp. <i>incertae sedis</i>	$\frac{1}{1}$		$\frac{1}{2}$	$\frac{1}{3}$			
Micropternodontine-like gen. and sp. <i>incertae sedis</i>				$\frac{1}{1}$			
<i>Aethomylos simplicidens</i>	$\frac{1}{3}$	$\frac{1}{1}$	$\frac{1}{4}$	$\frac{2}{9}$			

FRIARS FORMATION						
	Mission Gorge Localities		Tierra Santa Localities	Kennedy Locality	Old Mission Locality	Murphy Cyn. 2 Locality
	V-68116	V-6873	V-71183	V-71175	V-71216	V-6888
Species ³	V-68116	V-6873	V-71183	V-71175	V-71216	V-6888
<i>cf. Apatemys</i> sp.						
?Palaeoryctine gen. and sp.						$\frac{1}{11}$
<i>Sespedectes singularis</i>	$\frac{2}{6}$	$(\frac{2}{2})$		$(\frac{2}{2})$		
<i>cf. Proterixoides davisi</i>	$\frac{1}{1}$					
<i>Cryptolestes vaughni</i>	$\frac{1}{3}$	$(\frac{2}{2})$	$\frac{3}{12}$	$\frac{1}{1}$	$\frac{1}{1}$	$\frac{1}{1}$
<i>cf. Nyctitherium</i> sp.						
<i>Centetodon</i> spp.	$\frac{1}{1}$		$\frac{2}{3}$			$\frac{1}{1}$
<i>Batodonoides powayensis</i>				$\frac{1}{1}$	$\frac{1}{1}$	
?Apternodontine gen. and sp.						
Erinaceoid-like gen. and sp. <i>incertae sedis</i>				$\frac{1}{2}$	$\frac{1}{1}$	
Micropternodontine-like gen. and sp. <i>incertae sedis</i>						
<i>Aethomylos simplicidens</i>	$\frac{1}{1}$		$\frac{1}{4}$			

³The occurrence of each species at any given locality is indicated by a fraction whose denominator represents the total number of identified specimens from that locality and whose numerator represents the minimum number of individuals necessary to account for the total number of specimens (method after McKenna 1960a).

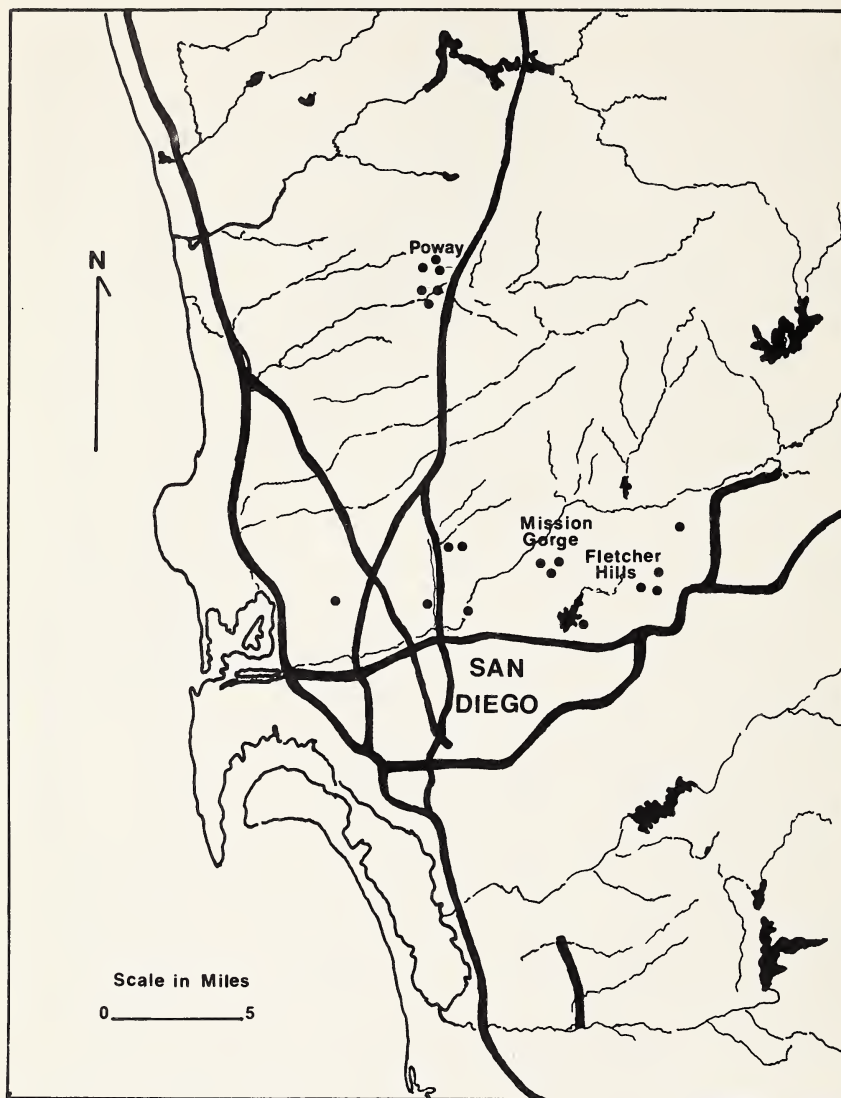


FIGURE 1. Map of the greater San Diego area showing approximate location of all localities (closed circles) except loc. V-72088 listed in Table 1. Heavy black lines represent major highway systems.

of *S. singularis*. Mandibles and maxillae of *S. singularis* from V-72088 may have been carried for only a short distance before they were buried. Maxillae were quickly destroyed, and their teeth were scattered prior to deposition and/or winnowing out by subsequent current action. More durable mandibles successfully resisted initial breakup and subsequent reworking by current action. The situation at V-72158 may have been somewhat different. Many skeletal and dental elements initially fragmented by high energy currents could have collected in the relatively calmer waters represented by the fine-grained matrix at V-72158. If currents were sufficiently strong to fragment both mandibles and maxillae, a random concentration of these scattered elements in current eddies might result in the approach to a 50-50 ratio of upper and lower dentitions of *C. vaughni* observed at V-72158.

There is some evidence that elements of *Sespedectes singularis* were carried for a shorter distance than other small mammalian remains at V-72088. Many isolated rodent teeth of comparable size are scattered throughout the fossiliferous unit; however, rodent mandibles which are at least as strong as those of *S. singularis* are extremely rare. Hence, the rodent material was probably carried a greater distance prior to deposition than bones and teeth of *S. singularis*. Conceivably, remains of *Sespedectes* may have been transported and buried in a site not far from where the animal spent most of its life.

Overall faunal comparisons of a detailed nature between V-72088 and V-72158 have not yet been completed. Excellent lower vertebrate samples from both V-72088 and V-72158 are now being studied by Mr. Richard Schatzinger. It is anticipated that this material will yield significant information on the environments represented. Rather uncommon fish bones and shark and ray teeth are intermixed with terrestrial vertebrate remains at V-72088. Beds containing marine invertebrate fossils are also found in close stratigraphic and lateral proximity to the fossiliferous unit at V-72088. None of these elements are known from V-72158. This suggests that V-72088 may represent an estuarine environment, while V-72158 probably represents an environment further inland.

The "crude" observations presented above do not conclusively prove my interpretation of the microhabitat represented by locality V-72088. The possibilities that 1) *Sespedectes singularis* lived close to the site of burial, and 2) V-72088 may represent an estuarine environment, are merely suggested as hypotheses for future testing by analysis of biological, taphonomic, and sedimentological data.

Another less easily tested hypothetical explanation for the insectivore faunal compositions at V-72088 and V-72158 is that *S. singularis* may have exhibited a broad range of food habits, and thus excluded insectivores competing for the same food resources. I doubt that *S. singularis* would have come into direct competition with most of the kinds of insectivores common to V-72158. There may, however, have been competition between *Cryptolestes vaughni* and *Sespedectes singularis*. The animals are subequal in size, are more abundant than other insectivores in the fauna, and rarely, if ever, are found in the same localities. The dentitions of the two genera are similar in many adaptations, although the molars of *Sespedectes* have more bulbous cusps of lower relief and appear to be better adapted for a crushing mode of occlusion. The difficulty here lies in the lack of predictive value that a particular

dental morphology may have for revealing the true feeding habits of the animal with that dental morphology. Many mammals such as rodents possess highly specialized dental and masticatory features yet show natural acceptance of a wide variety of foods (see Landry 1970). Furthermore, analogies presently cannot be drawn from living hedgehog-like forms because the feeding habits of these creatures in their natural habitat are so poorly known.

METHODS

The dental nomenclature employed here follows that of Rich (1971:4) who slightly modified dental terminology proposed by Van Valen (1966:7-9).

All specimens were measured on an Ehrenreich Photo Optical "Shopscope." Measurements were in millimeters and were rounded off to the nearest one-hundredth of a millimeter. The following orientations for measuring cheek teeth (see Fig. 2) were used in this report:

Anteroposterior axis ("A-P" axis):

Lower posterior premolars—long axis of tooth.

Lower molars—line drawn through the apices of the metaconid and the entoconid.

Upper posterior premolars—line extended from anteriormost point of the anterolabial lobe to the posteriormost point of the metastylar lobe.

Upper molars (M^{1-2})—line drawn through the apices of the paracone and metacone.

Upper molars (M^3)—line drawn at right angles to a line which divides the tooth into equal anterior and posterior halves.

Length:

Lower posterior premolars—total length of crown; i.e., greatest dimension measured parallel to "A-P" axis.

Lower molars—total distance from the anterior face of the paraconid to the back of the talonid along a line parallel to the "A-P" axis (anterior cingulum not included in measurement).

Upper posterior premolars and upper molars—greatest dimension parallel to the "A-P" axis of tooth.

Width:

Lower posterior premolars—widest part of crown; greatest dimension measured at right angles to "A-P" axis.

Lower molars—two width measurements: trigonid width, talonid width, widest part of each of these sections of the crown measured at right angles to "A-P" axis.

Upper posterior premolars and upper molars—two measurements: anterior width, distance from the labialmost point of the anterolabial corner of the crown to the lingualmost point of the protocone; posterior width, distance from pos-

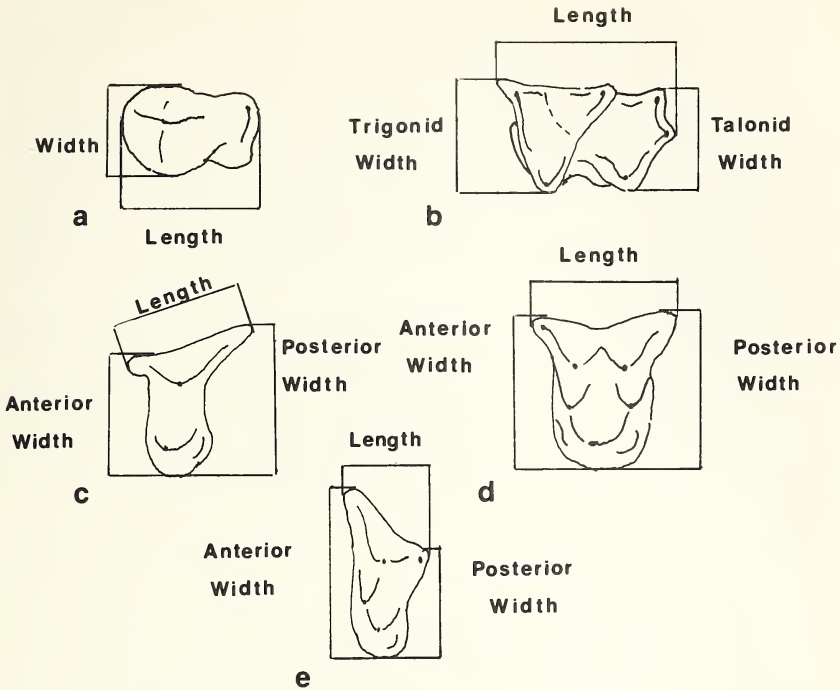


FIGURE 2. Occlusal view of diagrammatic cheek teeth showing orientations for measurements; a. lower posterior premolar, b. lower molar, c. upper posterior premolar, d. upper molar (M^1 or M^2), e. upper molar (M^3).

terolabialmost point of metastylar lobe to lingualmost point of protocone; both width measurements taken at right angles to the "A-P" axis.

The following abbreviations appear in this report:

N.	-number of observations (sample size)
O.R.	-observed range of variation
M.	-arithmetic mean
S.D.	-standard deviation
S.E.	-standard error of the mean
C.V.	-coefficient of variation
AMNH	-Department of Vertebrate Paleontology, American Museum of Natural History
CM	-Carnegie Museum
LACM	-Los Angeles County Museum of Natural History
LACM (CIT)	-specimens originally in the California Institute of Technology now housed in Los Angeles County Museum of Natural History
NMNH	-National Museum of Natural History, Smithsonian Institution
UA	-University of Alberta Paleontological Collection
UCMP	-University of California Museum of Paleontology, Berkeley
USNM	-United States National Museum, Smithsonian Institution
YPM	-Yale Peabody Museum

SYSTEMATICS

COMMENTS ON INSECTIVORE CLASSIFICATION

Various authors have noted the acute difficulty in classifying insectivores (see Romer 1968; Butler 1972; Dawson 1967). Due to the great present and past diversity of insectivores, their long evolutionary history, the poor quality and scarcity of fossils from crucial time periods and geographic areas, and the variety of interpretations that have arisen in insectivore taxonomy, the order defies definition and under the present concept is probably an unnatural group (see Butler 1972, for an excellent critical review of the problem).

This report is not intended as a comprehensive review of insectivore systematics. Such a study, which should include an attempt toward a phyletic classification of the order, is sorely needed. However, since the classification endorsed in this paper does not precisely conform to that in any published study, a general discussion of insectivore systematics is required. The following arrangement of higher categories is recognized in this report (taxa described in this paper have been assigned to those families indicated by an asterisk):

Order Proteutheria Romer 1966

- Family + Leptictidae Gill 1872
- Family + Pantolestidae Cope 1884
- Family + Ptolemaiidae Osborn 1908
- Family + Apatemyidae* Matthew 1909
- Family + Palaeoryctidae* Winge 1917

Order Insectivora Illiger 1811

Suborder Erinaceomorpha Butler 1956, 1972

- Family + Adapisoricidae* Schlosser 1887, (Van Valen 1967)
- Family Erinaceidae Fischer von Waldheim 1817
- Family ? Dimylidae Schlosser 1877

Suborder Soricomorpha Butler 1956, 1972

Superfamily Soricioidea Fischer von Waldheim 1817

- Family + Geolabididae McKenna 1960
- Family + Plesiosoricidae Winge 1917
- Family Solenodontidae Gill 1872
- Family + Micropternodontidae Stirton and Rensberger 1964
- Family + Nyctitheriidae* Simpson 1928, (Robinson 1968)
- Family Soricidae Fischer von Waldheim 1817
- Family + Nesophontidae Anthony 1916
- Family + Apternodontidae* Matthew 1910

Superfamily Talpoidea Fischer von Waldheim 1917

- Family Talpidae Fischer von Waldheim 1917

Suborder Tenrecomorpha Butler 1972

Superfamily Tenrecoidea Gray 1821

- Family Tenrecidae Gray 1821

Superfamily Chrysochloroidea Gray 1825

- Family Chrysochloridae Gray 1825

Illiger, in 1811, recognized a family Subterranea comprising moles, shrews, and hedgehogs. The name Insectivora was bestowed on this group by de Blainville in 1816.

The original descriptions of *Tupaia*, *Ptilocercus*, *Macroscelides*, *Petrodromus*, *Rhynchocyon*, and *Cynocephalus* in the first half of the 19th century prompted attempts to subdivide the order into natural categories. Haeckel (1866) created the insectivore suborders Lipotyphla—for those animals (shrews, moles, and hedgehogs) which lacked an intestinal caecum, and Menotyphla—for those animals (tree shrews, elephant shrews, and flying lemurs) in which the caecum was present. The concept Menotyphla (excluding the flying lemurs, separated by Gill in 1872 as the order Dermoptera) carries little, if any phylogenetic meaning. Many similarities between macroscelidids and tupaiids, such as the presence of a caecum, large jugals, fused pubic symphyses, and well-developed orbital wings of the palatine bones are likely primitive eutherian characters and thus are of little use in demonstrating relationships between the two groups. Significant differences between the two families in such features as brain and placental morphology far outweigh any of the above-listed similarities. I endorse Butler's (1972) recognition of the separate orders Macroscelidea and Scandentia (to include tupaiids) as a realistic taxonomic solution.

The lipotyphlan concept, on the other hand, seems well founded. A nucleus of living families, the Erinaceidae, Talpidae, Soricidae, Solenodontidae, Tenrecidae, and Chrysochloridae, comprise what appears to be a natural, though very broad, grouping on the basis of a number of shared-derived characters (cited by Butler 1972). In all these families an intestinal caecum is absent, the jugal bones are small or absent, there is an expansion of the maxillary bones into the orbital region of the skull replacing the palatines in that region, the mobile proboscis is moved by a series of specialized muscles which influence the form of the skull, the basisphenoid bone is the major component of the auditory bulla (although an ossified bulla is not present in soricids), the pubic symphysis is either reduced or absent, and there is no medial internal carotid artery.

A number of fossil groups, the Adapisoricidae, Micropternodontidae, Nesophontidae, Nyctitheriidae, Apternodontidae, Geolabididae, and Plesiosoricidae can, with varying degrees of confidence, be allied with the living lipotyphlans but the evidence for such allocations are mainly dental. A few of these families are, however, represented by excellent cranial material, and an argument for their affinity with Recent forms seems quite tenable.

Butler (1972) recognized the above living and extinct families as members of the order Lipotyphla and relegated several enigmatic insectivore families (Palaeoryctidae, Plagiomenidae, Apatemyidae, Pantolestidae, and Leptictidae) to the order Proteutheria (earlier recognized as a suborder by Romer 1966, and Van Valen 1967). Butler's (1972) action precludes formal usage of the order Insectivora. I see no compelling reason against equating Insectivora with Butler's (1972) Lipotyphla and retaining the former well known in the literature. The Insectivora would thus have a more restricted definition than under former usage, but such action would serve to demonstrate the doubtful ordinal affinities of the proteutherian families.

Order Proteutheria—There is little doubt that the Proteutheria is an artificial and presently indefinable category, and a purely phyletic classification would not recognize the unity of this order. Pending phyletic approach, I have followed Butler (1972) in allocating the Palaeoryctidae, Leptictidae, Apatemyidae, and Pantolestidae to the Proteutheria. Butler (1972) also included the Plagiomenidae in this

group, but I regard plagiomenids as provisional members of the Dermoptera in accordance with dental evidence reaffirmed by Rose (1973) and others.

Van Valen's (1967) concept of the Proteutheria differs strongly from the one presented here in his inclusion of tupaiids, zalambalestids, anagalids, paroxyclaenids, and pentacodontids within the suborder and in his recognition of the Palaeoryctidae as a family of his new order of mammals, the Deltatheridia (Van Valen, 1966). As is stated above, there is a case for excluding the Tupaiidae from the Insectivora. Szalay and McKenna (1972) have marshalled evidence for the recognition of a separate order, Anagalida, to include both anagalids and zalambdalestids. Zalambdalestids have specialized features in the cranium, feet, and dentition which suggest a close relationship between this group and lagomorphs (Van Valen 1964, Szalay and McKenna 1971). Whatever their affinities, the Anagalida seems to have diverged very early in the evolution of the Eutheria. In their bunodont molar construction, pentacodontids are more reminiscent of condylarths than insectivores. Pentacodontids are also unique in specializations of the posterior premolars. Van Valen (1967:231) noted the similarities in molar construction between certain pentacodontids and erinaceoids (e.g. *Proterixoides*). Such similarities are likely due to convergence as *Proterixoides*, *Sespedectes* and some related genera are highly specialized in molar morphology, although their relationship to more generalized adapisoricids can be demonstrated on the basis of other dental features (Novacek, MS.). Crusafont and Russell (1969) dispute Van Valen's (1965) alliance of paroxyclaenids with *Procerberus*, pointing out similarities of these animals with the condylarths, *Promioclaenus*, *Ellipsodon*, and *Oxyacodon*. Perhaps, as Rich (1971) has suggested, the Paroxyclaenidae should be regarded as *Eutheria incertae sedis*.

MacIntyre (1966), McKenna (1969), Szalay (1968) and others have presented evidence against Van Valen's (1966) placement of the Palaeoryctidae within his order Deltatheridia. The importance of this family in understanding the differentiation of the Eutheria has long been recognized. The Palaeoryctidae as presently regarded is probably an unnatural category whose members are grouped together mainly on the basis of the common possession of dentitions specialized in a shearing or piercing mode of occlusion. There seems little evidence for a close relationship between *Didelphodus* and palaeoryctines. Late Cretaceous North American palaeoryctids (*Cimolestes*, *Batodon*, and *Procerberus*) contrast strongly in certain dental features, and different species may be related to apatemyids (Szalay 1968), others to geolabidids (McKenna, personal communication), and still others to palaeoryctines, taeniodonts, and creodonts (Lillegraven 1969). Unfortunately, all Cretaceous palaeoryctids (with the exception of some unpublished Mongolian Late Cretaceous forms now under study by Kielan-Jaworowska) are known only from dentitions.

Leptictids contrast broadly with lipotyphlans in a number of important characters: the primary component of the ossified bulla is entotympanic rather than basi-sphenoid, the medial branch of the internal carotid artery is present, the posterior permanent premolars are molariform, deciduous premolars are retained through much of an individual's lifetime and the leptictid manubrium is uniquely enlarged. Szalay (1968) and others regard the Leptictidae as an isolated group of archaic eutherians not closely related to other insectivores, except for perhaps pantolestids. However, the Leptictidae is the best represented of the early Tertiary insectivores and information

derived from such excellent fossil material might provide insight into the morphotypical plan for the Eutheria.

Order Insectivora—The breakdown of the Lipotyphla endorsed in this paper follows Butler's (1972) scheme. The one major departure here is the removal of the Talpidae from Soricoida to its own superfamily, Talpoidea. This action corresponds with Bugge's (1974) recognition of the phyletic isolation of the talpids based on specializations in the pattern of carotid arterial circulation. Butler (1956) has pointed out many derived similarities between soricids and talpids in cranial morphology, but there is an abundance of anatomical evidence to suggest that talpids diverged very early in the evolution of the Insectivora and may be only remotely related to soricids, though closer than chrysochlorids and tenrecoids (Novacek, unpublished).

Perhaps no insectivore category is as difficult to understand as the Erinaceoidea. This highly heterogeneous superfamily contains many problematic genera. As is the usual case, confusion is greatest regarding primitive members. Two families were recognized by Van Valen, the Erinaceidae and the Adapisoricidae. Adapisoricids are difficult to differentiate from the Erinaceidae, the Hyopsodontidae, the Pentacodontidae, the Tupaiidae, and the Plesiosoricidae. Van Valen did not define this family other than to state (1967:272) that the included genera "... are sufficiently different from the Erinaceidae that familial distinction seems useful." Van Valen included four subfamilies within the Adapisoricidae, the Nyctitheriinae, Geolabidinae, Adapisoricinae, and Creotarsinae. He admitted (1967:272) that the assignments of many of the genera within these four subfamilies were provisional.

Robinson (1968) removed the Nyctitheriinae from the Adapisoricidae and raised it to familial rank. Robinson's concept of Nyctitheriidae, however, was notably different from the original one of Simpson (1937) in that the former included within it three subfamilies. The stem subfamily was the Nyctitheriinae consisting of the type genus *Nyctitherium*, its alleged ancestor *Leptacodon*, and a former soricoid, *Saturninia*. To this Robinson added the mole-like (in adaptive specializations, not in affinities) Micropternodontinae and the Geolabidinae. Robinson recognized only two of the eight genera included in the Geolabidinae by Van Valen (1967).

I favor Robinson's (1968) establishment of the family Nyctitheriidae, but I do not agree with his inclusion of the Geolabidinae within that family. Contrary to Robinson's contention (1968:134) the upper molars of geolabidines are not structurally close to those of *Leptacodon tener*, the alleged basal member of the Nyctitheriidae. Also the geolabidine P_4 is strongly contrasting to those of all nyctitheriines. I cannot accept the statement of Szalay and McKenna (1971:288) that nyctitheres (*sensu* Robinson) are derived from Cretaceous palaeoryctid stock via the late Cretaceous genus *Batodon*. *Batodon* was sufficiently specialized in dental construction to rule out the likelihood of its close relationship with *Leptacodon tener* and related nyctitheriines. *Batodon*, however, may be a primitive geolabidine as suggested by McKenna (personal communication).

The subfamily Geolabidinae has been subjected to major supraspecific revision since the time of Van Valen's classification. Szalay and McKenna (1971) relegated *Opisthopsalis* (a junior synonym of *Sarcodon*) and *Hyracolestes* to the Deltatheridiidae. They regarded *Praolestes* as a zalambdalestid genus belonging to their new order Anagalida. *Stilpnodon* is too poorly represented for assignment to any family

with certainty, but its P_4 construction is markedly different from that of all other geolabidine genera recognized by Van Valen. Robinson (1968) has recently reported that the type species of *Myolestes* (*M. dasypelix*) is referable to a new species of *Nyctitherium*.

The remaining geolabidine genera, *Centetodon*, *Embassis*, and *Geolabis* are the subjects of a major nomenclature controversy. McKenna has suggested (personal communication) that they are probably all synonymous, but varied opinions have been expressed as to which name has priority (see, for instance, McKenna 1960b; Clark 1966). Lillegraven and McKenna are currently reviewing the Geolabidinae and have made progress toward solving this nomenclatorial problem and refining the interspecific taxonomy of the group. One of their suggestions (*personal communication*) is that *Centetodon*, the earliest name, should have priority. Pending results of their study, I have referred to geolabidine material in this report as *Centetodon* sp.

A problem still remains concerning the broader affinities of the Geolabidinae. Although the members of this group (*Centetodon* and closely related, probably synonymous genera) resemble erinaceid-like forms in aspects of the dentition, they show a number of distinctive dental and cranial specializations (see McKenna 1960b). McKenna (*personal communication*) has suggested that geolabidines may be closely related to palaeoryctids like *Batodon*. I favor removing the Geolabidinae from the Adapisoricidae and raising the Geolabidinae to familial rank, as Butler has proposed (1972). Butler (1972) has remarked that geolabidines show a number of derived similarities with *Solenodon* and soricids and the allocation of this group to the Soricoidae seems reasonable.

With the exclusion of the above categories, there remains within the Adapisoricidae only the Creotarsinae and the Adapisoricinae. The latter subfamily has been the subject of major modification. Of the six genera included by Van Valen (1967) within the Adapisoricinae, only one, *Adapisorex*, seems to be definitely referable to the subfamily and the validity of this category is doubtful (see Clemens 1973:37, for a recent summary of the problem).

Van Valen (1967:272) conceded that the Creotarsinae lacked unity but could not be subdivided. The Creotarsinae is indefinable on purely morphological grounds, and I do not recognize the subfamily in this report. A subdivision of the Adapisoricidae seems unjustified until better material is available.

ORDER PROTEUTHERIA
FAMILY APATEMYIDAE
SUBFAMILY APATEMYINAE
GENUS *APATEMYS* MARSH
APATEMYS cf. *BELLUS* MARSH

Figure 3

Referred specimens.—left P_1 (or P_2), UCMP 101440; left lower incisor, UCMP 101623.

Locality.—UCMP loc. V-72158.

Description.— P_1 (or P_2 , see West 1973:19) is single-rooted and procumbent with a bladelike crown. The labial face of the blade is strongly concave. A small,

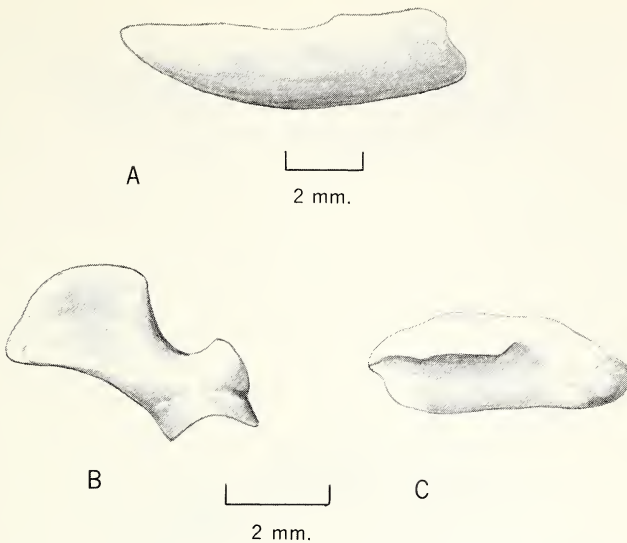


FIGURE 3. *Apatemys*, cf. *A. bellus*, left lower incisor UCMP 101623; a. labial view. Left P_1 (or P_2), UCMP 101440; b. labial view, c. occlusal view.

distinct cusp is present at the posteriormost region of the crown. Dimensions of P_1 (or P_2) are: length = 5.15, width = 1.96; lower incisor (UCMP 101623), length = 9.31, width = 1.91.

Remarks.—the bladelike P_1 (or P_2) (UCMP 101440) is highly characteristic of Eocene-Oligocene apatemyids. It compares closely in size with the homologous tooth of *Apatemys rodens* (described as a P_3 in Gazin 1958: 88-89). West (1973) has recently made all species of *Apatemys*, including *A. rodens* and *A. downsi* from the Sespe Formation (Gazin 1958), junior synonyms of *A. bellus*. The San Diego specimen may represent a geographic extension of *A. bellus*. However, since the major criteria used in apatemyid taxonomy are exclusive of P_1 (P_2) or incisor morphology, there exists the possibility that the San Diego specimens are referable to a new species of *Apatemys*. The P_1 (P_2) of the Oligocene *Sinclairiella* differs from UCMP 101440 in lacking a posterior accessory cusp.

FAMILY PALAEORYCTIDAE
SUBFAMILY ?PALAEORYCTINAE
GENUS AND SPECIES INDET.

Figure 4

Referred specimen.—left mandible fragment with M_{2-3} , UCMP 96081.

Locality.—UCMP loc. V-6888.

Description.— M_2 has a relatively very tall trigonid. The bladelike paraconid is lower than the protoconid and the metaconid is lingual to the lowest point of the

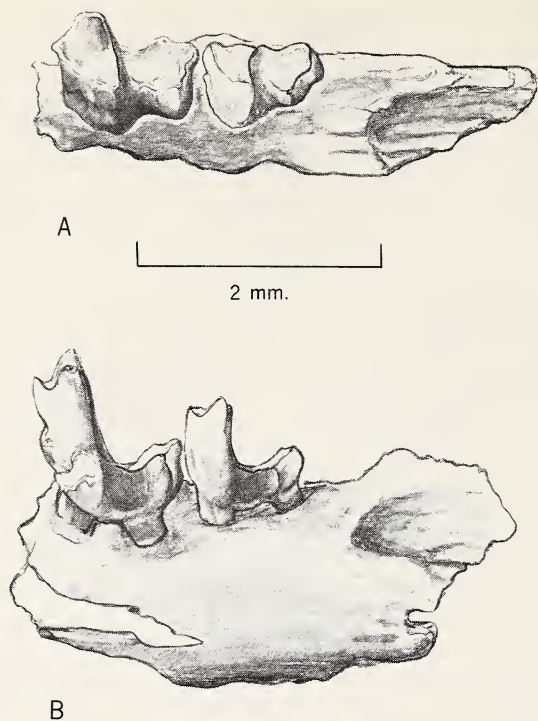


FIGURE 4. *Palaeoryctine* gen. and sp., left mandible fragment with M_{2-3} , UCMP 96081; a. occlusal view, b. labial view.

protocristid, and is slightly labial to the apex of the protoconid. A narrow anterior cingulum dips steeply ventrolabial. The talonid is elongate and narrower than the trigonid. The hypoconulid is the highest cusp of the talonid, is situated slightly closer to the entoconid than to the hypoconid, and is strongly produced posteriorly. The laterally compressed entoconid is situated more anteriorly than the hypoconid. The crista obliqua contacts the protoconid labial to the protoconid-metaconid juncture. Dimensions of the M_2 are: length = 1.22, trigonid width = 0.77, talonid width = 0.61.

M_3 is similar in morphology but is considerably reduced relative to M_2 . The trigonid is also lower relative to the talonid. The talonid is relatively narrower than that of M_2 . The small entoconid is set more posteriorly than the hypoconid. The hypoconulid is more posteriorly produced than in M_2 . Dimensions of M_3 are: length = 1.04, talonid width = 0.47.

Remarks.—the lower molars in UCMP 96081, with their high transverse trigonids and low narrow talonids, resemble those of *Palaeoryctes* (Matthew 1913), *Pararyctes* (Van Valen 1966), and *Cimolestes propalaeoryctes* (Lillegraven 1969). They are distinct from the M_2 and M_3 's of these genera primarily in that 1) the trigonids are of slightly lower relief; 2) the paraconid is much higher relative to the protoconid and metaconid, as is the lingual opening of the prefossid; 3) the antero-lingual face of the protoconid is lower and less steep; 4) the talonid in M_2 is antero-

posteriorly more elongated and relatively wider; and 5) the M_3 is considerably less tall and smaller in overall dimensions than the M_2 . Although the molars in UCMP 96081 were effective shearing and piercing elements, the above differences suggest that they do not approach the "zalambdodont" condition as closely as do the molars of *Pararyctes*, *Palaeoryctes*, or *Cimolestes propalaeoryctes*.

The affinities of the San Diego animal are unclear. It is an Eocene form which, despite its late appearance, possesses features in the molars less specialized than Paleocene palaeoryctines and the Cretaceous *Cimolestes propalaeoryctes*. Hypothesized derivation of the species represented by UCMP 96081 from *Palaeoryctes*, *C. propalaeoryctes* or similar forms would require reversals in trends from those which occurred in the evolution of *Palaeoryctes*. Due to the lack of more complete material, I can only tentatively assign this San Diego insectivore to the Palaeoryctidae as a probable new genus showing affinities most closely with *Palaeoryctes*, *Pararyctes*, or *Cimolestes (propalaeoryctes)*.

While the San Diego animal represented by UCMP 96081 is not excluded from the rather broad definition of the Didelphodontinae (see Van Valen 1966:68), it shows stronger tendencies toward the dental specializations of the Palaeoryctinae. I would refer the San Diego species to the Palaeoryctinae with reservations, acknowledging that more complete evidence may refute this action.

Some students may suggest that the species described here be given a formal taxonomic name. I feel that the assignment of a new generic and specific name on the basis of specimen UCMP 96081 alone could prove to be an impediment to its future study. Insectivore taxonomy is already overburdened with problematic genera represented by one or two teeth.

ORDER INSECTIVORA
SUBORDER ERINACEOMORPHA
SUPERFAMILY ERINACEOIDEA
FAMILY ADAPISORICIDAE
SESPEDECTES STOCK
SESPEDECTES SINGULARIS STOCK

Sespedectes singularis is by far the most abundant insectivore in the San Diego collections. There are, at present, more than 297 isolated teeth and over 43 jaws with two or more teeth referable to this species. Stock (1935) first described *S. singularis* from the Eocene Sespe Formation located north of Los Angeles, in Ventura County, California. No significant morphological differences between specimens from the San Diego localities and the Sespe localities have been recognized. A detailed description and a consideration of the affinities of *Sespedectes* are provided elsewhere (Novacek, MS.).

PROTERIXOIDES STOCK
PROTERIXOIDES DAVISI STOCK

This species is a rarity in San Diego deposits; it is represented by only four specimens. Stock (1935), however, reported that *Proterixoides davisi* was very

abundant in the Sespe localities. *P. davis* bears a strong similarity to *Sespedectes singularis*, differing from the latter only in its much larger size and in details of upper premolar and molar morphology. There is little doubt that the two species are closely related. For a description and analysis of material referable to *Proterixoides*, see Novacek (MS.).

CRYPTOLESTES NEW GENUS

Etymology.—Crypt-G.: hidden, secret; referring to the cryptic identity of material representing this genus. Until the type specimen was recovered, all M²'s were identified as ?leptictid upper molars, and lower teeth were referred to a new species of *Sespedectes*. -lestes G.: robber, following the tradition of the usage of this term to designate small insectivorous animals.

Type species.—*Cryptolestes vaughni*.

Diagnosis of genus.—*Cryptolestes* is distinguished from all other adapisoricid genera by the following combination of characters. DP⁴ is three-rooted with a paracone, metacone, protocone, prominent metastylar lobe, and lingual cingula. P³ is not greatly reduced relative to P⁴ and is similar in morphology to it. The upper molars, especially M², are transverse teeth with sharp cusps. The paracone and metacone have steep labial faces. The labial lobes, particularly the parastylar lobe of M², are prominent. A distinct precingulum is consistently present on M¹⁻³. The hypocone of M¹⁻² is well-developed, but lower than the protocone. The paraconule and metaconule are distinct and subequal in size. The postmetaconule wing continues labially as a metacingulum. M³ has a paraconule. DP⁴ is heavily worn by the time the upper molars erupt. There are three mental foramina in the mandible.

CRYPTOLESTES VAUGHNI NEW SPECIES

Figures 5-8, Table 2

Etymology.—named in honor of Peter P. Vaughn, vertebrate paleontologist and teacher.

Holotype.—UCMP 103912, a left maxillary fragment with DP⁴ - M² and unerupted P⁴.

Type locality.—V-71211, Mission Valley Formation.

Referred Specimens.—left mandible with M₁₋₃ and alveoli for C - P₄, UCMP 96155; isolated teeth and tooth fragments: P³, UCMP 101316 and 101437; six P⁴'s, UCMP 96123, 101128, 101292, 101543, 101605, 101615; 11 M¹'s, UCMP 99320, 99427, 101015, 101023, 101322, 101409, 101441, 101531, 101610, 103895, 104407; 22 M²'s, UCMP 96111, 96148, 96439, 96441, 99354, 99387, 99438, 101044, 101120, 101317, 101463, 101473, 101477, 101486, 101505, 101546, 101624, 101636, 101646, 101698, 103904, 104798; 11 M³'s, UCMP 96109, 101049, 101069, 101107, 101124, 101125, 101422, 101499, 101587, 101696, 101744; 9 P₄'s, UCMP 96153, 96409, 101411, 101432, 101437, 101502, 101585,

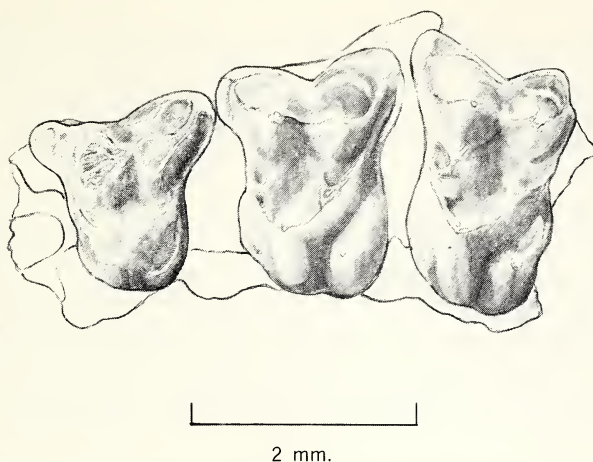


FIGURE 5. *Cryptolestes vaughni*, new genus and species. Holotype, UCMP 103912, left maxillary fragment with DP⁴-M² and unerupted P⁴; occlusal view.

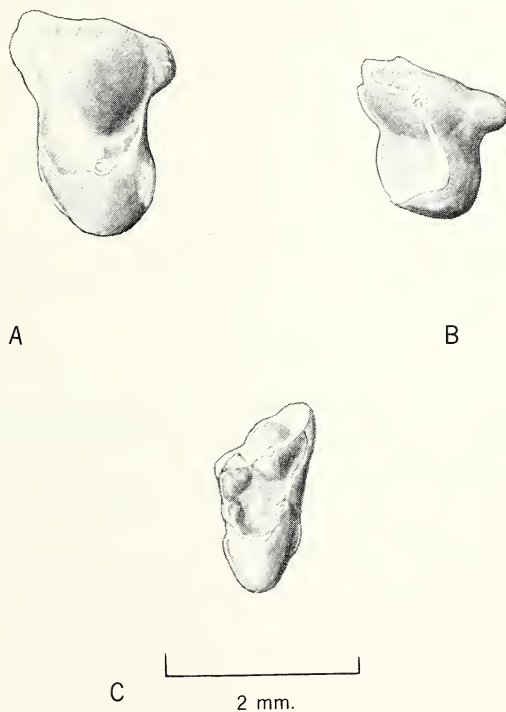


FIGURE 6. *Cryptolestes vaughni*, new genus and species; a. right P⁴, UCMP 101128; b. right P³, UCMP 101437; c. right M³, UCMP 101587. All views occlusal.

101608, 101609; 9 M_1 's, UCMP 96143, 101020, 101051, 101074, 101414, 101429, 101485, 101535, 101606; 16 M_2 's, UCMP 101026, 101030, 101039, 101050, 101072, 101088, 101090, 101104, 101323, 101419, 101433, 101462, 101478, 101542, 101618, 103967; 11 M_3 's, UCMP 96445, 101034, 101075, 101105, 101108, 101117, 101313, 101328, 101456, 101500, 104409; edentulous jaw fragment, UCMP 104413.

Localities.—UCMP locs. V-6840, V-6873, V-6882, V-68116, V-71175, V-71176, V-71180, V-71183, V-71216, V-72157, V-72158, V-72176, V-73188.

Diagnosis of species.—as for genus.

Description.— DP^4 - in the type specimen (UCMP 103912) is a heavily worn three-rooted tooth with a paracone, metacone, and protocone, prominent metastylar lobe, anterior accessory cuspule, and lingual cingula. There is no evidence of a paraconule or metaconule. The presence of a hypocone is suggested by a swelling in the posterolingual corner of the crown and the rise of the postcingulum in this region.

The three-rooted P^3 is slightly wider than long with a high, robust paracone. There is a strong metastylar crest and a minute accessory cuspule at the base of the anterior face of the paracone. The protocone is lower than the paracone and situated lingual and slightly anterior to it. Wear is most notable on the apices of the protocone, paracone, and anterior accessory cuspule, the posterior face of the protocone, and the metacrista.

P^4 is strikingly similar to P^3 in structure differing from the latter only in its larger size and in having a more oblique anterior margin, a relatively more prominent anterior accessory cuspule, and narrow lingual cingula.

The upper molars have bilobate labial margins and sharp, conical cusps. In M^1 , the metacone and paracone are well separated and subequal in height. The metaconule and paraconule are well-developed, and the postmetaconule wing continues labiad as the metacingulum. A narrow precingulum is present. The protocone is situated directly lingual to the paracone. There is a distinct hypocone approximately two-thirds the height of the protocone. The postcingulum terminates at the apex of the hypocone. M^2 is similar to M^1 except that it is more transversely elongate and anteroposteriorly compressed, it has a more prominent parastylar lobe, a weaker metastylar lobe, and a more anteroposteriorly compressed hypocone. M^3 differs from M^{1-2} in having a weak metacone situated at the posterolabial corner of the crown and in the absence of a metaconule.

P_4 has a tall protoconid, weak metaconid and vestigial paraconid. The P_4 talonid is a transverse ridge with two minute cusps.

The lower molars have subequally tall metaconids and protoconids, reduced and blade-like paraconids, and narrow anterior cingula. In M_{1-2} the entoconid and hypoconid are subequal in height and situated directly opposite each other. The hypoconulid is a weak cusp positioned nearly directly between, but slightly posterior to, the entoconid and hypoconid. M_3 is reduced relative to M_{1-2} . The M_3 trigonid is anteroposteriorly elongate. The hypoconulid is produced posteriorly and situated closer to the entoconid than to the hypoconid. The hypoconulid and entoconid are taller than the hypoconid. Wear on the hypoconids precedes that on the other molar cusps.

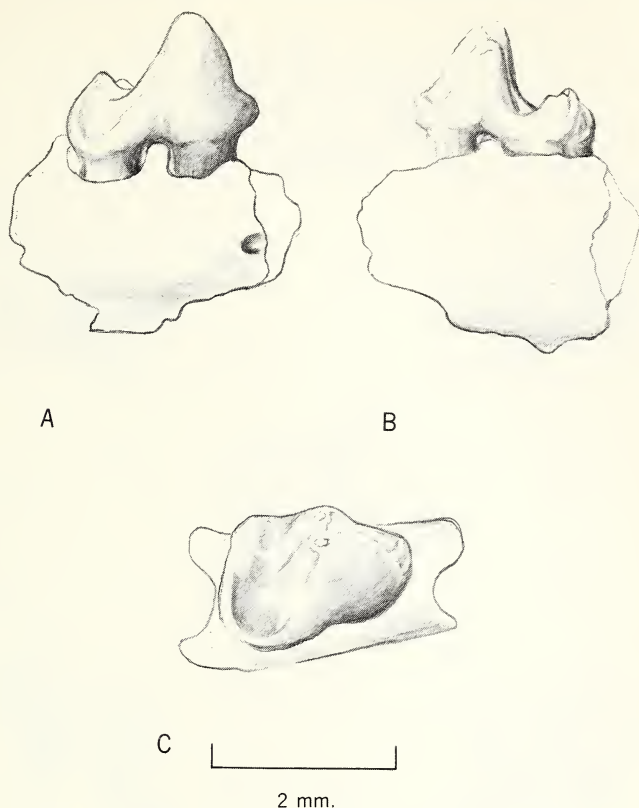


FIGURE 7. *Cryptolestes vaughni*, new genus and species, right mandible fragment with P_4 , UCMP 101609; a. labial view, b. lingual view, c. occlusal view.

The mandible has three mental foramina; the anteriormost opening is the largest. The posteriormost mental foramen is situated below the posterior alveolus of P_3 .

Remarks.—*Cryptolestes vaughni* and *Sespedectes singularis* show a close similarity in certain dental features. In both forms, P^3 is not greatly reduced relative to the P^4 and is similar in morphology to it. Among erinaceoids in which the upper premolar dentition is known, only *Tupaiodon* (Matthew and Granger 1924), *Litolestes* (Simpson 1936), and the primitive erinaceid *Galerix socialis* (Engesser 1972), possess such a well-developed P^3 . The P_4 's in both San Diego genera are strikingly similar although *Cryptolestes* differs in having a bicuspid P_4 talonid. P^4 differences between *C. vaughni* and *S. singularis* are truly minor. The lower molars of *Sespedectes* are generally indistinguishable from those of *Cryptolestes*.

Such similarities do not extend to comparisons between the upper molars in both genera. *Cryptolestes* differs markedly from *Sespedectes* in the possession of

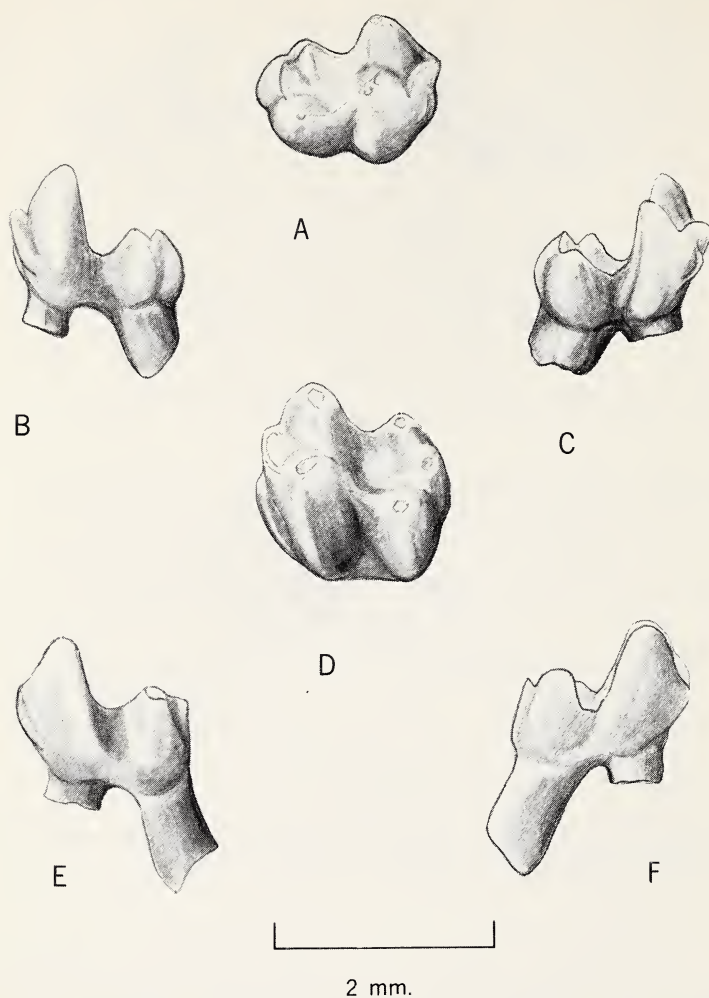


FIGURE 8. *Cryptolestes vaughni*, new genus and species, right M_3 , UCMP 101328; a. occlusal view, b. lingual view, c. labial view. Left M_2 , UCMP 101542; d. occlusal view, e. labial view, f. lingual view.

the following characters of the upper dentition: 1) the upper molars, especially $\bar{M}^2$, are transversely wider and more anteroposteriorly compressed, with sharper cusps; 2) the paracone and metacone are taller, more conical cusps, and their labial faces are clearly steeper than their lingual faces; 3) the labial lobes, particularly the parastylar lobe of M^2 , are more prominent; 4) a distinct precingulum is consistently present on M^{1-3} ; 5) the hypocone in M^2 is anteroposteriorly more compressed than in

TABLE 2

Measurements of teeth referred to
Cryptolestes vaughni new genus and new species

Element	N.	O.R.	M.	S.D.	S.E.	C. V.
P ₄						
length	7	1.75-1.91	1.81	0.058	0.022	3.2
width	7	1.01-1.18	1.09	0.064	0.024	5.9
M ₁						
length	9	1.55-1.78	1.66	0.073	0.024	4.4
trigonid width	9	1.12-1.37	1.26	0.066	0.022	5.2
taloid width	8	1.10-1.38	1.24	0.094	0.033	7.6
M ₂						
length	15	1.40-1.68	1.57	0.100	0.026	6.4
trigonid width	16	1.23-1.47	1.34	0.077	0.019	5.7
taloid width	17	1.16-1.42	1.27	0.078	0.019	6.2
M ₃						
length	13	1.45-1.75	1.55	0.086	0.024	5.6
trigonid width	13	0.89-1.17	1.05	0.151	0.042	14.7
taloid width	12	0.75-1.01	0.86	0.070	0.020	8.2
P ⁴						
length	4	1.61-1.75	1.65	0.070	0.035	4.3
anterior width	5	1.92-2.04	1.98	0.055	0.025	2.8
posterior width	6	1.72-2.08	1.91	0.123	0.050	6.4
M ¹						
length	6	1.50-2.35	1.86	0.334	0.136	17.9
anterior width	3	1.86-2.03	1.95	0.086	0.049	4.4
posterior width	3	2.03-2.23	2.15	0.108	0.062	15.0
M ²						
length	12	1.14-1.48	1.39	0.101	0.029	7.3
anterior width	10	1.99-2.51	2.23	0.203	0.064	9.1
posterior width	15	1.72-2.30	2.11	0.047	0.046	8.4
M ³						
length	10	0.88-1.23	1.08	0.103	0.033	9.6
anterior width	10	1.65-2.07	1.86	0.152	0.049	8.2
posterior width	10	1.06-1.43	1.29	0.026	0.035	8.5

the homologous tooth of *Sespedectes*; 6) the postmetaconule wing continues labially as a metacingulum; 7) DP⁴ is heavily worn at the time the upper molars are erupted. These comparisons demonstrate that *Cryptolestes* is closer in upper molar morphology to certain adapisoricids than to *Sespedectes* and *Proterixoides*.

The upper molars of *Cryptolestes*, *Macrocranium* (Tobien 1962), *Entomolestes* (*nitens*) (McKenna 1960a), *Messelina* (Tobien 1962), *Litolestes*, and *Scenopagus*

(McKenna and Simpson 1959) are distinguished from those of *Sespedectes* and *Proterixoides* in their common possession of sharper paracones and metacones with steeper labial faces, a relatively lower hypocone, a distinct paraconule, subequal in size to the metaconule, and a metacingulum formed by the labial continuation of the postmetaconule wing.

In all of the above genera except *Scenopagus* and possibly *E. nitens*, the molars are less transversely developed with weaker labial lobes than in *Cryptolestes*.

Macrocranium can be distinguished from *Cryptolestes* by the narrower stylar shelf, more labially situated conules, and weaker precingula in its upper molars. It is separated from both *Cryptolestes* and *Sespedectes* by its reduced P^3 and elongate M_3 .

Messelina differs from *Cryptolestes* in much the same features as does *Macrocranium*, but is more clearly separated in its possession of a P_4 with a prominent paraconid and a basined talonid.

The upper molars of *Scenopagus mcgrewi*, noted above, are much more transverse with a stronger parastylar and metastylar lobe than those of *Cryptolestes*. In addition, *Scenopagus* has a smaller hypocone and more lingually situated conules.

Showing a close resemblance with *Cryptolestes* are the upper molars referable to cf. *Entomolestes nitens* by McKenna (1960a: 58-59). Except for the more lingual position of the conules, a slight difference in outline of the labial margin, and a weaker hypocone, the upper molars of *E. nitens* seem hardly different from those of *Cryptolestes*. For the present, cf. *E. nitens* must be distinguished by its possession of a P^4 with an incipient metacone and lower molars with relatively wider talonids.

Litolestes notissimus (Simpson 1936:24) demonstrates a striking resemblance between that genus and *Cryptolestes* in upper molar morphology. The only differences observed are the presence of a stronger parastylar lobe in M^1 , weaker parastylar lobes in M^{2-3} , and a weaker precingulum. *Litolestes* is separated by the possession of an incipient metacone on P^4 and a smaller P^3 . There is a possible close relationship between *Litolestes*, *Entomolestes*, *Cryptolestes*, and *Sespedectes*.

It is evident that in certain dental characters *Cryptolestes* bridges the morphological gap between *Sespedectes* (and *Proterixoides*) and other adapisoricids. Indeed, *Cryptolestes* may be closer to the structure of the morphotypical ancestor of *Sespedectes* and *Proterixoides* than any other primitive erinaceoid known. Evolution of the latter two genera might have involved the loss of primitive characters, such as the second cuspule on the P_4 talonid, and a reduction of cutting elements in the cheek teeth, with an increased development of adaptations for a crushing mode of occlusion. Concomitant with these specializations came a change in the process and timing of tooth eruption. Unlike the condition in *Cryptolestes*, the eruption of the characteristic erinaceoid cutting P^4 is delayed in *Sespedectes*. It is possible to speculate that in *Sespedectes* the molariform DP^3 and DP^4 functioned with the molars as an extensive crushing battery for a significant part of the animal's life span. The evolution of *Cryptolestes* involved none of these modifications and certain primitive dental characters were retained.

SUPERFAMILY ?SORICOIDEA
FAMILY NYCTITHERIIDAE
SUBFAMILY NYCTITHERIINAE
GENUS *NYCTITHERIUM* MARSH 1872
CF. *NYCTITHERIUM* SP.

Figure 9

Referred specimens.—incomplete isolated right upper molars, UCMP 96085 and 101011.

Localities.—UCMP locs. V-71180 and V-72158.

Description.—UCMP 101011 is a damaged right molar missing the entire stylar shelf and most of the metacone. The protocone is nearly as tall as the paracone. The paraconule is situated more lingually than the metaconule. Two distinct wings diverge labially from each conule. The precingulum is narrow but distinct, extending from the anterolingual base of the protocone to a point below the most labial section of the preparaconule wing. A prominent postcingulum is strongly developed into a low hypocone. The apices of the protocone and paracone show slight wear.

A well-developed metacrista is the only notable feature in UCMP 96085 not preserved in UCMP 101011.

Remarks.—UCMP 96085 and 101011 are very close in structure to the upper molars of *Nyctitherium velox* from the middle Eocene (Bridgerian) of North America (Robinson 1968:132, Figs. 2, 6, specimens YPM 15251 and YPM 13515). The



2 mm.

FIGURE 9. cf. *Nyctitherium* sp., upper right molar, UCMP 101011; occlusal view.

San Diego specimens differ from *N. velox* upper molars only in being more antero-posteriorly compressed and in having a slightly more lingually projecting hypocone (evident in UCMP 101011). In these features UCMP 101011 resembles *Saturninia gracilis*, a former soricid relegated by Robinson (1968) to the Nyctitheriidae. No definite conclusions can be reached concerning this comparison due to the lack of more complete material. In short, UCMP 96085 and 101011 indicate the presence of a nyctithere, possibly congeneric with either *Nyctitherium* or *Saturninia*, in the San Diego Uintan fauna.

FAMILY GEOLABIDIDAE
SUBFAMILY GEOLABIDINAE
GENUS *CENTETODON* MARSH
CENTETODON SP.

Referred specimens.— P^4 , UCMP 101306; M^1 's, UCMP 101046, 101076, 101301, 101446; M^2 's, UCMP 99390, 101082, 101303, 101304, 101307; M^3 's, UCMP 101089; P_1 , UCMP 101309; P_4 's, UCMP 96127, 96137, 99321, 101070, 101081, 101084; M_1 's, UCMP 99321, 101055, 101305; M_2 's, UCMP 99431, 99434 101123, 101126, 101302; M_3 , UCMP 101083.

Localities.—UCMP locs. V-6888, V-68116, V-71180, V-71183, V-72157, V-72158.

Remarks.—The material referable to probably more than one species of *Centetodon* from the San Diego Uintan will be described by Lillegraven and McKenna in their forthcoming discussion of the genus.

***BATODONOIDES* NEW GENUS**

Etymology.—Bato-G., thorn, -don, G. tooth;-oides G., like; referring to the close resemblance to the genus *Batodon*.

Type species.—*Batodonoides powayensis* new species.

Diagnosis.—*Batodonoides* is a diminutive geolabidine significantly smaller than all other members of that subfamily. The lower dentition of *Batodonoides* is not significantly different from that of *Centetodon* except for its smaller size. The upper molars of *Batodonoides* distinguish this genus from all other geolabidines in the possession of the following combination of characters: high piercing cusps, a wide stylar shelf, a strong sharp metacrista, a prominent lingual paraconule, no metaconule, a narrow precingulum and postcingulum not connected across the lingual base of the protocone, a postcingulum developed into a minute hypoconal crest, and a single lingual root.

BATODONOIDES POWAYENSIS NEW SPECIES

Figures 10-12, Table 3

Etymology.—referring to the geologic and geographic origin; all specimens referable to the species found in beds of the Poway Group; type recovered in a locality near the town of Poway, California.

Type.—UCMP 96459, fragment of right mandible with P_4 and M_1 .

Type locality.—UCMP loc. V-71211, Mission Valley Formation.

Referred specimens.—fragments of mandibles with P_1 , UCMP 96457; P_4 's, UCMP 96431, 96432, and 101311; M_1 , UCMP 96403; M_{2-3} , UCMP 96448; isolated M_1 's, UCMP 96138, 96145; M^1 's, UCMP 96126, 96456; edentulous mandible fragments, UCMP 96087, 101458.

Localities.—UCMP locs. V-71175, V-71176, V-71181, V-71211, V-71216, and V-72158.

Diagnosis.—as for genus.

Description.—The anterior edge of the ascending ramus is nearly perpendicular to the horizontal ramus of the mandible. The depth of the jaw below the M_2 is approximately 0.95 mm. The posterior mental foramen is below the anterior root of P_4 . An anterior mental foramen is below an alveolus for the posterior root of P_2 in UCMP 101311. A low rounded horizontal ridge extends posteriorly from the base of the anterior border of the median face of the ascending ramus.

P_1 is double-rooted, blade-like, and laterally compressed. The main cusp projects anteriorly, forming a prominent, slightly blunted "nose." A minute posterior accessory cuspule is the most posterior element of the crown.

P_4 has a high trigonid dominated by the protoconid. Most of the labial face of the metaconid is fused to the protoconid, resulting in a steep posterior trigonid wall, broken only at its crest. A steeply descending paralophid extends anterolingual to the extremely low, well separated paraconid. A blunt shelf descends from the apex of the low paraconid curving around the base of the labial side of the paracristid. The talonid is laterally compressed and lingually shifted, leaving a broad and deep hypoflexid. A posterior cuspule is prominent and close to the center of the back of the talonid. Major wear occurs on the protoconid and the metaconid apices, the protocristid, the entire posterior trigonid wall (except for a narrow labial margin), the hypoflexid, and the anterolabial face of the posterior cuspule.

The trigonid of M_1 is high and curves lingually toward its apex more than does the trigonid of P_4 . The protoconid is higher than the metaconid. The median walls of the protoconid and the metaconid are fused nearly to the apex of the metaconid. The paraconid is low relative to the protoconid and the metaconid of M_1 but higher than the paraconid of P_4 . The paraconid anterolabial face is much higher than the talonid of P_4 . A short cingulum slopes ventrad at a steep angle on the anterolabial face of the paraconid. The talonid is narrower than the trigonid and has a deep basin.

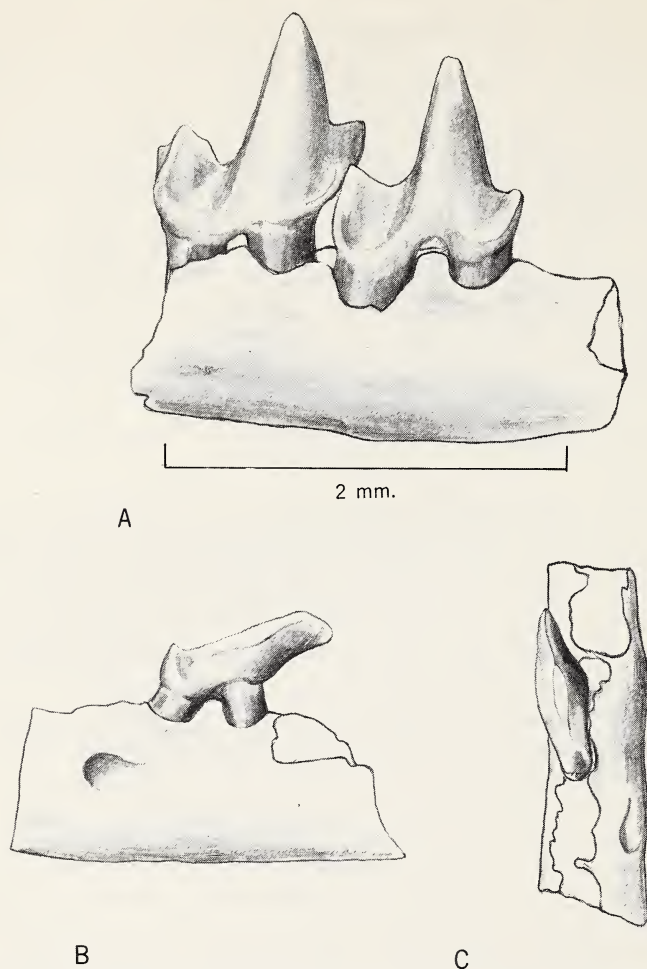


FIGURE 10. *Batodonoides powayensis*, new genus and species, Holotype, UCMP 96459, right mandible fragment with P_4 - M_1 ; a. labial view. Right mandible fragment with P_1 , UCMP 96457; b. labial view, c. occlusal view.

The hypoconid and the hypoconulid are subequal in height. The entoconid is the smallest cusp of the talonid. The hypoconulid is situated posterior and central to the hypoconid and entoconid. A crista obliqua joins the base of the posterior trigonid wall far below the lowest point of the protocristid. Wear on M_1 is similar to that on P_4 .

Only the talonid of M_2 is preserved (UCMP 96448). At the stage of wear observed, the apices of the closely appressed hypoconulid and entoconid are obscured.

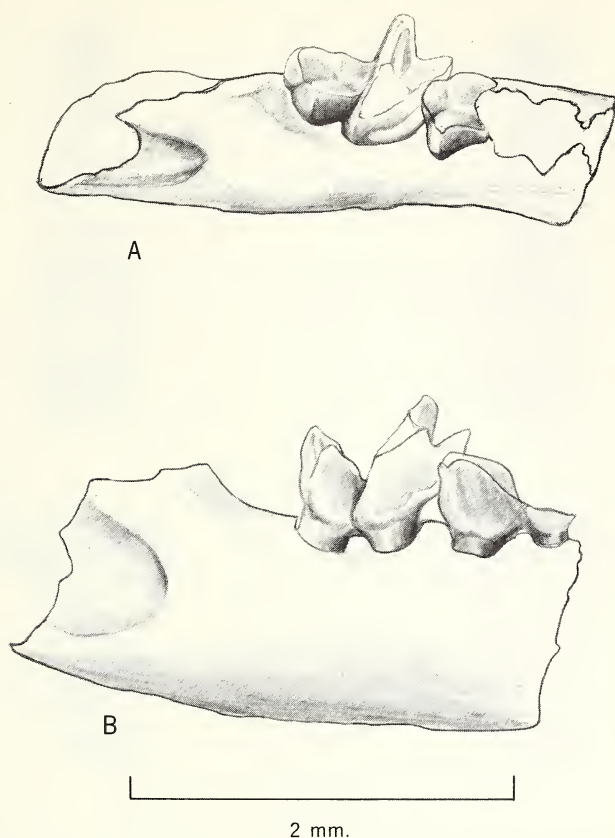


FIGURE 11. *Batodonoides powayensis*, new genus and species, right mandible fragment with partial M_2 and complete M_3 , UCMP 96448; a. occlusal view, b. labial view.

Both cusps are well separated from the hypoconid. The talonid appears to be slightly narrower than the damaged trigonid. There is pronounced wear on the steep labial surface of the entoconid and hypoconulid, and the anterolabial face of the hypoconid. Slight wear exists on the lingual face of the hypoconid.

In the only M_3 preserved (UCMP 96448), the apex of the protoconid is broken away. The talonid is more transversely compressed than those of M_{1-2} . The entoconid is undiscernible, being extremely weak, or possibly absent. The lingual rim of the talonid appears as an unbroken ridge which steeply descends from the apex of the prominent hypoconulid to the base of the posterior metaconid ridge. A hypoconid is present, but it is much lower than the hypoconulid. The trigonid is more acutely triangular in outline than that of M_1 . Wear patterns are similar to those in P_4 - M_2 mentioned above.

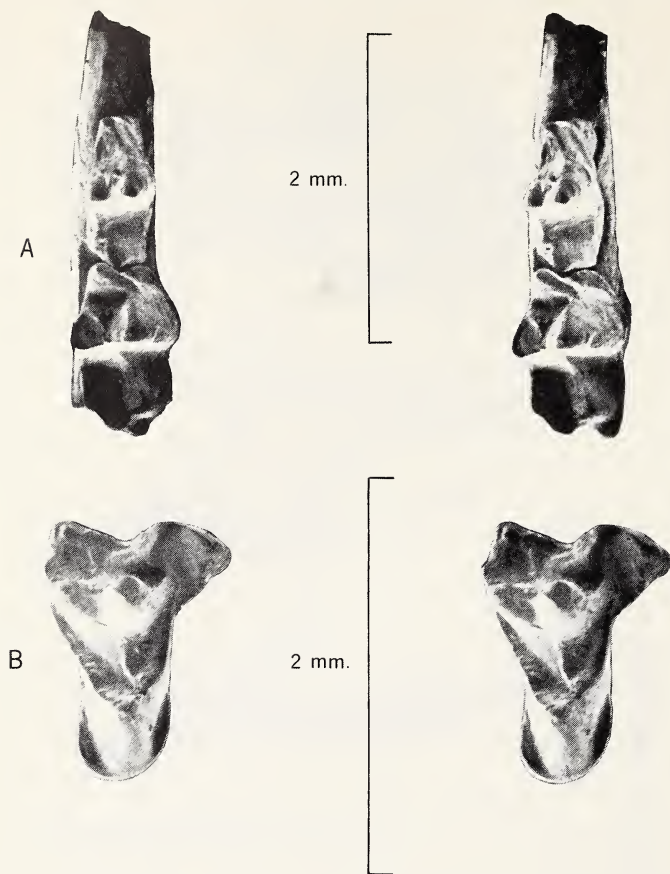


FIGURE 12. *Batodonoides powayensis*, new genus and species, a. Holotype, UCMP 96459, fragment of right mandible with P_4 - M_1 ; b. right M^1 , UCMP 96126. All views occlusal. Stereophotographs taken with scanning electron microscope.

The upper molars are transversely wide and anteroposteriorly compressed with high sharp cusps. The paracone is slightly higher than the subequal protocone and metacone. At late stages of wear, the metacone is considerably reduced in height relative to the paracone. The metacone is slightly posteriorly inclined. A very narrow precingulum extends from a point below the paraconule nearly to the lingual edge of the tooth. The postcingulum is developed into a minute hypoconal crest. The labial edge of the wide stylar shelf has an ectoflexus in its mid-region. There is an anteriorly projecting, cuspsate parastylar lobe. The paraconule is prominent and lingual, being situated high on the preprotocrista near the upper section of the protocone. A metaconule is absent. The high, sharp metacrista extends to the extreme posterolabial corner of the tooth. The paracrista is low and extends to the apex of the parastylar cusp. There is a vertical trough on the lingual face of the parastylar lobe. Major wear

TABLE 3

Measurements of teeth referred to
Batodonoides powayensis new genus and species

Element		Measurements				
P ₁	<u>96457</u> ⁴					
length	0.75					
width	0.29					
P ₄	<u>96459</u> (type)	<u>96432</u>	<u>96431</u>	<u>101311</u>		
length	0.90	0.91	0.92	0.93		
trigonid width	0.42	0.41	0.49	0.48		
talonid width	0.30	0.33	0.39	0.39		
M ₁	<u>96459</u> (type)	<u>96432</u>	<u>96138</u>	<u>96145</u>	<u>96403</u>	
length	0.99	1.00	1.00	1.04	1.05	
trigonid width	0.62	0.61	0.60	0.70	0.65	
talonid width	0.48	0.51	0.50	0.52	0.51	
<u>talonid width</u> trigonid width	0.78	0.83	0.84	0.74	0.79	
M ₃	<u>96448</u>					
length	0.84					
trigonid width	0.60					
talonid width	0.38					
<u>talonid width</u> trigonid width	0.64					
M ²¹	<u>96126</u>	<u>96456</u>				
length	0.95	1.01				
anterior width	1.29	1.15				
posterior width	1.33	1.26				

⁴All numbers are UCMP specimen numbers.

occurs on the apices of the paracone, metacone, the parastylar cusp, the metacrista and centrocrista, preprotocrista, postprotocrista, and labial face of the protocone. Definite shear abrasion can be seen on the anterior and the posterior faces of the trigon cusps, the anterior face of the paraconule, and the posterior wall of the metacrista.

Remarks.—The reference of UCMP 96126 and 96456 (both upper molars) to *Batodonoides powayensis* is not beyond question, but I believe it is supported by several observations. Both upper molar specimens are from localities in which lower teeth of *B. powayensis* were recovered. The only other insectivore teeth collected at these sites were much larger in size. Further, UCMP 96456 was found in the same locality (V-71211) as most of the lower dentitions representing this species, including the type. The teeth are nearly as long and slightly more than twice as wide as the lower molars. Direct manipulation shows that the upper molars occlude adequately with the M₁ of *Batodonoides*.

Functional significance of dental features.—The morphology of the upper and lower molars of *Batodonoides* suggests that occlusion at the beginning of the powerstroke was mainly orthal, followed by lingual movement of the lower molars during the late phases of the powerstroke. This latter movement produced transverse shear against the upper molars.

The relatively lingual position of the paracone and metacone increased the effective shearing surface of the labial prevallum and postvallum. There is a distinct preparaconule wing, providing a second cutting edge opposing the back of the trigonid which functioned in a later phase of the powerstroke. The lingual position of the paraconule in *Batodonoides* served to elongate the preparaconule wing and thus the effective area of this shearing surface. The protocone is transversely wide, anteroposteriorly compressed and transversely aligned with the paracone. Such a condition, as noted by Crompton (1971:70), may be viewed as an extension of the shearing surface of the preparaconule wing, and thus full advantage has been taken of transverse mandibular movement. Because of this specialization, the anterior face of the protocone would be in contact with the back of the trigonid at the end of the powerstroke. The hypoflexid in M_{1-3} of *Batodonoides* is deep and the talonid is laterally compressed, increasing the area of shear surface between the posterior wall of the trigonid and the anterior face of the paracone. This condition would also increase the amount of shear surface between the anterolabial face of the hypoconid and the postparacrista. Deep hypoflexids are often present in mammals in which the paracone is hypertrophied. The narrow precingulum in *Batodonoides* approaches the condition in *Didelphodus* (see Crompton 1971) in which the precingulum is entirely lacking. The precingulum provides an additional cutting edge for shear against the back of the trigonids at the end of the occlusal cycle. That the small hypoconal crest in *Batodonoides* actually ever came in contact with the small hypoconulid and entoconid is highly doubtful. It possibly served as a trap for ingested food. The lack of a metaconule in *Batodonoides* is highly interesting. I feel that the extreme reduction or loss of the metaconule allows for the occlusion of the protocone with the small talonid basin at the end of the powerstroke. It is interesting to note that insectivores with very reduced laterally compressed talonids (e.g., certain tenrecs, apternodontines, etc.) often lack conules.

Affinities.—The lower dentitions of *Batodonoides powayensis* are strikingly similar to those of *Centetodon* (= *Geolabis* see McKenna 1960b), differing mainly in their much smaller size. Since disparity in size is nearly always a poor criterion for separating taxa above the specific level, an allocation of *Batodonoides* to *Centetodon* based solely upon lower dentitions seems reasonable. However, upper molars of *Centetodon* differ from those referred to *Batodonoides* in having a narrower stylar shelf and (in latest Eocene and younger species) two lingual roots. Geolabidines show specialized cranial features, including the elongate snout and enlarged lacrimal foramen, which are highly diagnostic of the group (see McKenna 1960b:134). Until associated dentitions and cranial material referable to *B. powayensis* are known, the species cannot be assigned without question to the Geolabidinae. However, based upon the available evidence, the identification of *Batodonoides* as a distinct geolabidine genus seems the most appropriate.

Material referable to the Late Cretaceous species *Batodon tenuis* (see Lillegraven 1969; Clemens 1973) shows very close similarities, both in size and dental morphology, to *Batodonoides powayensis*. The comparative morphology and possible phyletic relationships of these two genera warrant careful consideration.

Examination of AMNH 58777, a lower jaw with P_{2-4} , M_{1-2} referable to *Batodon tenuis*, shows that that species is nearly identical to *Batodonoides powayensis* in morphology of the lower jaws and dentition. The only difference is the position of the posterior mental foramen below the anterior root of P_4 in *Batodonoides* and below the posterior root of P_4 in *Batodon*. An M_3 (UA 4081) tentatively referred to *B. tenuis* by Lillegraven (1969:84) differs from the homologous tooth in *B. powayensis* in its larger size and in its possession of a relatively wider talonid, a prominent entoconid, and a more salient hypoconulid. Regrettably there are no specimens representing either genus in which the M_3 is associated with teeth anterior to the M_1 .

Upper teeth of *Batodon tenuis* are poorly known. Lillegraven (1969:84) tentatively referred a maxillary fragment with an M^2 and a partial M^1 (UA 4081) to *B. tenuis*. The M^2 in this specimen shows a similarity to the upper molars of *Batodonoides* in having high cusps, a closely appressed paracone and metacone, narrow lingual cingula, a paraconule, a parastylar lobe of similar morphology, a weak paracrista, and a strong metacrista. However, the M^2 in UA 4081 differs from referred M^1 's of *Batodonoides* in that 1) the tooth is transversely wider; 2) there is a metaconule; 3) the precingulum is more elongate and is connected to the postcingulum across the lingual base of the protocone; 4) the stylar shelf is narrower; 5) the postcingulum is not developed into a hypoconal crest; 6) the ectoflexus is less deep; and 7) the paraconule is more labial relative to the apex of the protocone. These comparisons suggest that although the putative upper molars of both genera are similar in basic construction, they are easily distinguished.

Batodon was regarded as a didelphodontine palaeoryctid by Lillegraven (1969) and Clemens (1973), but McKenna, who is now restudying the phylogenetic relationships of *Batodon*, has suggested (*personal communication*) that this genus is an early geolabidine. This seems to be a tenable allocation in view of the strong similarities between *Batodon*, *Batodonoides*, and *Centetodon*. Further, I believe that the palaeoryctid like dental characters of these genera (particularly in *Batodon* and *Batodonoides*) are evidence for a close relationship between the Geolabidinae and palaeoryctids.

FAMILY ?APTERNODONTIDAE
SUBFAMILY ?APTERNODONTINAE
NEW GENUS AND SPECIES UNNAMED

Figure 13

Referred specimen.—isolated right M^2 , UCMP 96135.

Locality.—UCMP loc. V-71055. Mission Valley Formation.

Description.—The tooth is transversely wide and anteroposteriorly compressed. The metacone is much lower than the paracone and protocone, which are subequal

in height. The metacone is fused with the posterior face of the paracone for most of its height, a condition commonly known as "protozalambdotony." In posterior view, the metacone has the appearance of a shoulder on the steeply rising metacrista. The posterior faces of the metacone and metacrista form the sheer postvallum of the tooth. The labial faces of the paracone and metacone are strongly concave. The styler shelf is wide, and there is a deep ectoflexus along its labial margin. The parastylar lobe projects anteriorly and is much more prominent than the metastylar lobe. Although the metacrista is somewhat higher than the paracrista, both structures are sharp and prominent. Conules, a precingulum, a postcingulum, and a stylocone are absent. There is a wear facet on the apex of the protocone. Prominent wear is present on the preprotocrista and postprotocrista. The paracone and metacone apices, the paracrista, and the metacrista show only slight wear. Dimensions of UCMP 96135 are: length = 0.75; anterior width = 1.13; posterior width = 1.00.

Remarks.—The above described semi-zalambodont characters of this tiny specimen suggest a possible affinity with the middle Eocene to middle Oligocene apternodontine genera, *Oligoryctes* Hough (1956:538-541) and *Apternodus* Matthew (1903). However, UCMP 96135 is distinct from the upper molars of those genera in the possession of a weak metacone, the lack of a strong stylocone, the presence of a prominent protocone, and the absence of cingula external to the anterior and posterior faces of the paracone. In addition, *Apternodus* is significantly larger than the animal from the Eocene of San Diego.

McKenna (*personal communication*) brought to my attention a small M¹ (C M 13761) from the Green River Formation, Wyoming, referable to a new middle Eocene apternodontine genus, *Eoryctes* (*nomen nudum* Romer 1966:381 *ex* McKenna MS.), which is being described in his (unpublished) study of the Apternodontinae. The M¹ of this animal is somewhat intermediate in structure between the San Diego specimen and the upper molars of *Oligoryctes* and *Apternodus* in the possession of a large protocone; however, like the latter two genera, it lacks a metacone and it has both an anterior and a posterior paracingulum.

Although the San Diego animal is approximately contemporaneous with other known apternodontines, the protozalambodont condition of the paracone and metacone suggests that it is structurally primitive in the dentition to forms such as *Oligoryctes*, *Apternodus*, and *Eoryctes*.

Geolabidine upper molars are protozalambodont in the partial fusion of the paracone and metacone, but they are distinct from UCMP 96135 in their much larger size and in having a hypocone supported by a distinct root (in latest Eocene and later species), a precingulum, weakly developed conules in some forms, and usually a stylocone.

The upper molars of *Palaeoryctes puericensis* differ from UCMP 96135 in the following ways. The upper molars of *Palaeoryctes* are transversely wider and more anteroposteriorly compressed, with relatively higher cusps. The paracone and metacone in *Palaeoryctes* are fused nearly to their apices, and are subequal in height. The styler shelf is strongly crested in the region of the parastylar and metastylar lobes in the upper molars of *Palaeoryctes* (see Van Valen 1966:140). It is Van Valen's

interpretation (1966) that *Palaeoryctes puerensis* and its allies represent an extremely specialized offshoot of the palaeoryctid basal stock, and the alleged affinities between *Palaeoryctes* and living tenrecoids have been seriously questioned by McDowell (1958:208). However, the question of a possible relationship between *Palaeoryctes* and apternodontines requires closer examination. It seems unlikely that *Palaeoryctes* and the species represented by UCMP 96135 are closely related, but such an arrangement cannot be totally dismissed based on the present meager evidence.

Among recent zambododont insectivores, the West African tenrecoid genus *Potamogale* shows the closest similarities in morphology of the upper molars to UCMP 96135. Like the latter, *Potamogale* has a weak metacone and a prominent protocone, a feature which is unique among living tenrecoids. However, *Potamogale* seems more specialized toward zambododonty than the San Diego specimen in the labial position of the metacone resulting in the V-shaped outline of the ectoloph characteristic of zambododont upper molars. There is also a distinct stylocone in *Potamogale*. Whether the presence of a metacone in *Potamogale* represents an advanced specialization or the retention of a primitive ancestral character is a controversial matter (for opposing arguments, see McDowell 1958:180, and Van Valen 1966:footnote,51).

One final statement should be made regarding the size of UCMP 96135. This upper molar approaches the diminutive size of the upper molars of *Suncus etruscus*, the smallest living mammal. UCMP 96135 is representative of a truly tiny insectivore.

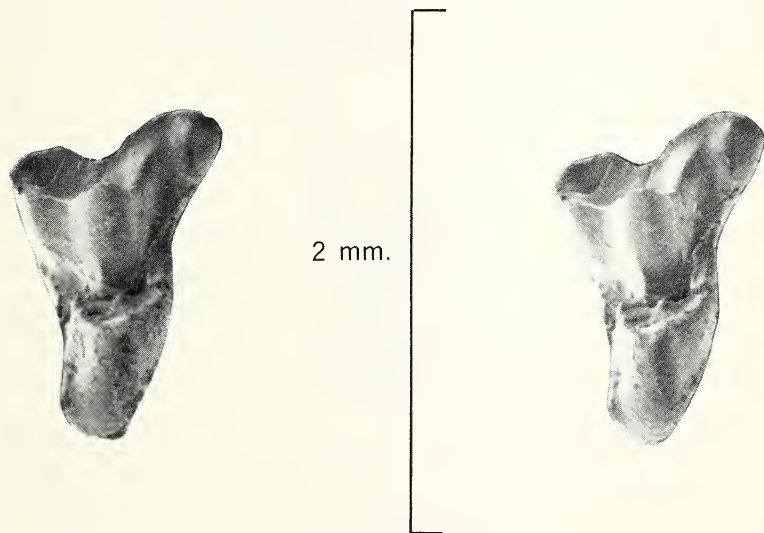


FIGURE 13. ?Apternodontine genus and species, unnamed, right upper molar ($M^2?$), UCMP 96135; occlusal view. Stereophotographs taken with scanning electron microscope.

INSECTIVORA INCERTAE SEDIS
ERINACEOID-LIKE GENUS AND SPECIES

Figure 14, Table 4

Referred specimens.—left M¹, UCMP 101420; fragmentary right M¹, UCMP 101059; right fragmentary M², UCMP 101626; right M³, UCMP 101497; right upper molar fragment, UCMP 101654; right lower molar, UCMP 101617.

Localities.—UCMP locs. V-71180, V-72157, V-72158.

Description.—M¹ is a robust tooth with a conical paracone and metacone which are subequal in height and are well separated by a deep valley. A very prominent metastylar lobe projects labiad and slightly posteriorly. The anteriorly projecting parastylar lobe is much smaller than the metastylar lobe. The metacrista is well-developed. Both the paraconule and the metaconule are distinct and are subequal in basal dimensions. The robust protocone is subequal in height with the paracone and metacone, about twice the height of the hypocone, and is situated directly lingual to the paracone. The precingulum is narrow. The hypocone is a large cusp with a prominent swelling at the posterolingual corner of its base. The apex of the hypocone is positioned well lingual to that of the protocone. UCMP 101626, a probable M², differs from M¹ in having a much weaker metastylar lobe.

M³ (UCMP 101497) is damaged, missing its entire posterior margin. The parastylar lobe projects prominently anterolabial. The labial tooth margin is straight. There is no metastylar lobe. The paracone is exceedingly higher than the tiny conical metacone. The paraconule is large with a well-developed preparaconule wing but without a postparaconule wing. The metaconule is lower and much more lingually

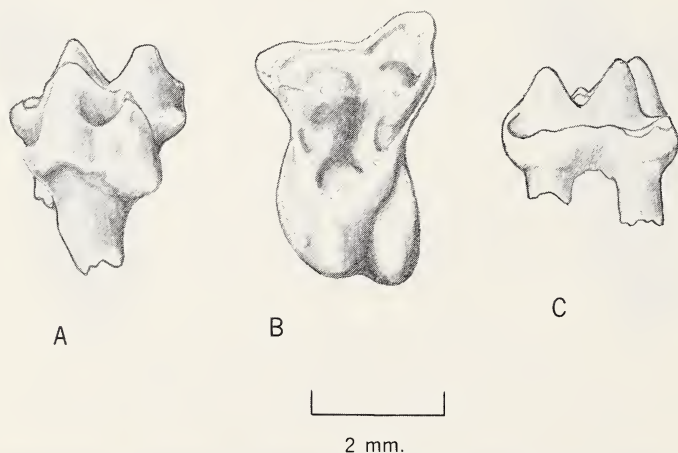


FIGURE 14. Erinaceoid-like genus and species, left M¹, UCMP 101420; a. lingual view, b. occlusal view, c. labial view.

positioned than the paraconule. The protocone is lower than the paracone and is anteriorly recumbent. A narrow precingulum is present.

UCMP 101617, a probable M_2 , has an erect trigonid slightly less than twice the height of the talonid. A small anteroposteriorly compressed paraconid is present. A narrow anterior cingulum extends for a short distance along the base of the prevallid. The metaconid is approximately equal in height to the protoconid and is situated directly lingual to it. The crista obliqua contacts the posterior trigonid wall below and slightly labial to the lowest point of the protolophid. The small hypoconulid is situated slightly posterior to and equidistantly between the entoconid and the hypoconid.

Remarks.—The perplexing problems involved in identifying new insectivore species on the basis of a few isolated teeth are fully realized in a consideration of the affinities of the above described material. These specimens resemble homologous teeth of a number of insectivore taxa, but their assignment even at the familial level is unclear.

The molars show the following adapisoricid characters: 1) a large hypocone not connected to the postprotocrista by a ridge; 2) conical paracones and metacones well separated at their bases and subequal in height; 3) a comparatively low trigonid; 4) a weak, anteroposteriorly compressed paraconid; 5) a small, centrally placed hypoconulid; 6) wear patterns which do not suggest a great development of vertical shearing.

TABLE 4

Measurements of teeth referred to
Insectivora incertae sedis, Erinaceoid-like gen. and sp.

Element	Measurements	
M^1	<u>UCMP 101420</u>	<u>UCMP 101059</u>
length	3.16	---
anterior width	3.86	4.23
posterior width	4.63	---
M^2	<u>UCMP 101626</u>	
length	---	
anterior width	---	
posterior width	3.55	
M^3	<u>UCMP 101497</u>	
length	1.95	
anterior width	3.10	
posterior width	2.55	
Lower Molar	<u>UCMP 101617</u>	
length	2.71	
trigonid width	2.26	
talonid width	2.14	

The animal represented by the above described specimens shows a close similarity to the adapisoricid genera *Macrocranion tupaiodon* (see Tobien 1962) and *Tupaiodon morrissi* (AMNH 19134, described by Matthew and Granger 1924:1-2), but is easily distinguished from these forms in the prominence of the hypocone and the metastylar spur.

Ankylodon (Patterson and McGrew 1937) from the Oligocene of North America, was placed in Plesiosoricidae by Van Valen (1967:264), but Butler (1972:259) regards this genus as the last surviving member of the Adapisoricidae. The previously unknown upper dentition of *Ankylodon annectens* is now being described by Lillegraven and McKenna (*personal communication*). In the prominence of the metastylar lobe, UCMP 101420 approaches the extreme enlargement of this structure in the M¹ of *Ankylodon*. A resemblance between the two homologous teeth is also seen in the strong, lingually situated hypocone. However, *Ankylodon* is distinct in several major features, including sharper, more anteroposteriorly compressed cusps on the upper molars, taller and sharper lower molar cusps, and evidence of a greater overall emphasis upon vertical shear during occlusion. It is possible that *Ankylodon* arose from an early Uintan adapisoricid-like insectivore with a more generalized morphology resembling that of the above described San Diego teeth.

MICROPTERNODONTINE-LIKE GENUS AND SPECIES

Figure 15

Referred specimen.—a left probable M₂ with the lingual face of the trigonid destroyed, UCMP 101308.

Locality.—V-72158, Mission Valley Formation.

Description.—The trigonid of this tooth is high and quite compressed anteroposteriorly. The protoconid is a sharp cusp, higher than the paraconid, with a steep, slightly overhanging labial edge. A deep prefossid separates the paraconid from the protoconid. A prominent anterior cingulum descends the prevallid at a steep angle. The talonid is elongate with a completely enclosed basin. The hypoconid is more prominent than the entoconid. The hypoconulid and entoconid are approximated but not "twinned." The hypoconulid projects strongly posteriorly. Measurements of the tooth are: length = 1.54; talonid width = 0.89.

Remarks.—UCMP 101308 shows a close resemblance to the M₂ in NMNH (USNM) 186837, a mandible fragment with M₁₋₃ from the Little Pipestone Springs localities of the early Oligocene of Montana. Emry (*personal communication*) tentatively identified NMNH 186837 as ?*Micropternodus*. UCMP 101308 differs from NMNH 186837 mainly in having a relatively wider talonid and more extended anterior cingulum.

Geolabidine M₁₋₂'s differ from UCMP 101308 in having less transversely widened prevallids, trigonids which curve lingually toward the apex, a less steeply sloping anterior cingulum, and less posteriorly projecting hypoconulid.

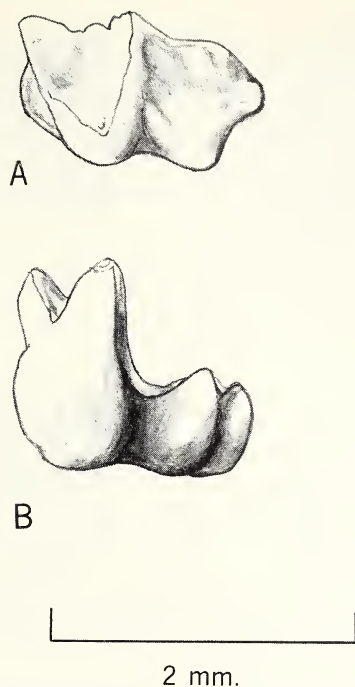


FIGURE 15. Micropternodontine-like genus and species, left Mx, UCMP 101308; a. occlusal view, b. labial view.

The Micropternodontinae (of Stirton and Rensberger 1964) is a specialized insectivore subfamily showing mole-like adaptations and nyctitheriid affinities (see Robinson 1968). The group makes its first appearance in the early Oligocene, or possibly the late Eocene (see Black and Dawson 1966), but it is conceivable that micropternodontine history goes back to early Eocene times. Certain characters in the lower molars of *Micropternodus* as diagnosed by Stirton and Rensberger (1964) are lacking in UCMP 101308. Nevertheless, the latter may, pending more complete material, represent an early Uintan member of the Micropternodontinae.

AETHOMYLOS NEW GENUS

Etymology.—Aeth, Gr., irregular, curious, unusual; mylos, Gr., molar.

Type species.—*Aethomylos simplicidens*.

Diagnosis.—*Aethomylos* is distinguished from all known insectivore genera by the following combination of dental characters. The upper molars are triangular in outline, where viewed from a labial aspect. They have an ectoflexus, a very narrow to absent stylar shelf, a conical paracone, metacone, protocone, and a large deeply

excavated protofossa. There are no conules, hypocones, or precingula. The P_4 or DP_4) is an elongate molariform tooth with a large talonid basin and three talonid cusps. There is a "step-like" structure on the back of the trigonid. The lower molars have low trigonids with shelf-like paraconids. There is no anterior cingulum. A sharp turn in the paralophids lends to the trigonids a semi-rectangular outline when viewed from a dorsal aspect. The talonid has a deeply excavated basin bordered by three cusps. The hypoconid is much higher than the hypoconulid.

AETHOMYLOS SIMPLICIDENS NEW SPECIES

Figures 16-19, Tables 5-6

Etymology.—Simplicidens, L., simple tooth; refers to the simplicity of the molar morphology of this species.

Type.—UCMP 96133, left upper molar.

Type locality.—V-71183. Friars Formation.

Diagnosis.—as for genus.

Referred specimens.—upper molars (and possibly deciduous premolars), UCMP 96133, 96443, 99428, 101047, 101066, 101068, 101312, 101590, 104178; P_4 , UCMP 96088, 101077; M_{1-2} 's, UCMP 96092, 96453, 101067, 101119, 101625, 101645, 101750; M_3 , UCMP 101630.

Localities.—UCMP locs. V-68116, V-71180, V-71183, V-71211, V-72157, V-72158.

Description.—All upper teeth listed above show the following morphology. The teeth, in occlusal view, have the vague appearance of an equilateral triangle. An ectoflexus is present. The stylar shelf is extremely narrow to absent. The paracone and metacone are conical cusps with steeper labial faces than lingual faces. The metacone is lower than the paracone and is widely separated from it by a deep valley. The metacone is situated at the posterior edge of the crown and is not bordered posteriorly by a metacingulum. A narrow paracingulum is present. The protofossa is large and deeply excavated. The protocone is anteriorly recumbent and transversely compressed with a steep labial face and a bulbous lingual face. There is no hypocone, but a swelling in the posterolingual corner of the crown is present in most specimens. Lingual cingula are absent. Beyond these basic characters there is marked variation in the morphology of the labial margin of the crown and the metastylar and parastylar spurs among different teeth in the dental arcade.

UCMP 96088 and 101077, both probable P_4 's (or DP_4 's), are elongate molariform teeth. The paraconid is low and well separated from the protoconid and the metaconid. The protoconid is much higher than the metaconid. The metaconid is situated slightly more posteriorly than the protoconid. There is a step-like structure on the back of the trigonid in UCMP 101077. As a result of wear, the top of the step slants ventrolabial from a high point behind the lingualmost margin of the posterior face of the metaconid to the base of the crown directly behind the labial margin of the

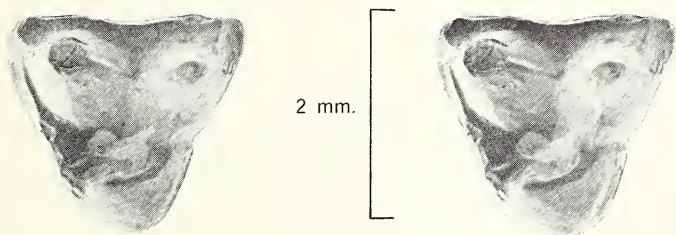
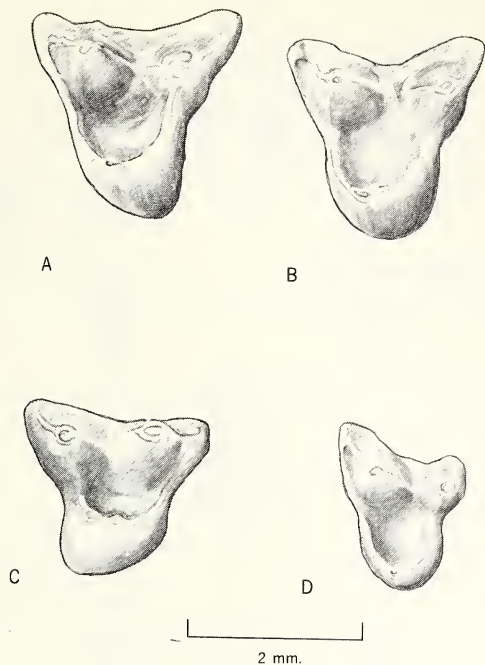


FIGURE 17. *Aethomylos simplicidens*, new genus and species, left upper cheek tooth, UCMP 101066. Occlusal view. Stereophotograph taken with scanning electron microscope.

protoconid. The talonid has a well-developed deeply excavated basin. The three talonid cusps and their connecting ridges form a rim, which, in occlusal view, is rounded rather than sharply angular at the corners.

All lower molars have the following basic features: The trigonid is not exceedingly high in comparison to the talonid and its posterior wall leans forward. The paraconid is shelf-like in appearance. There is no anterior cingulum. The paralophid descends directly anteriorly from the apex of the protoconid for a short distance

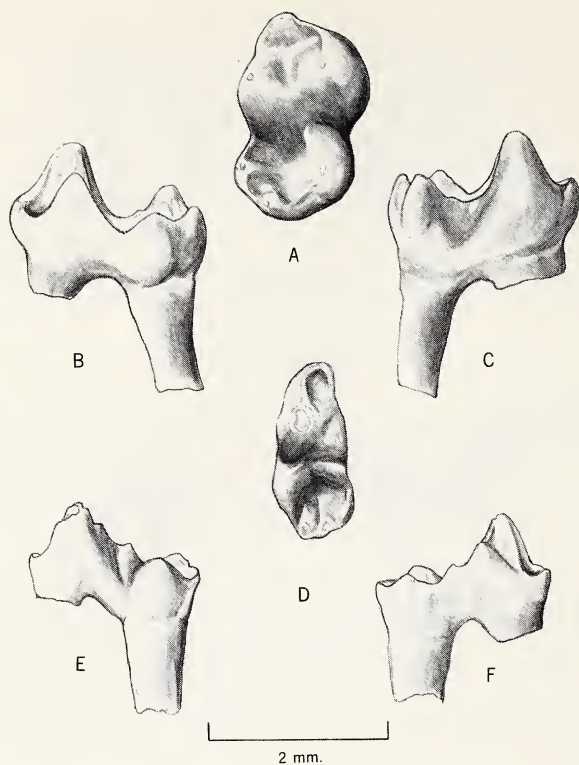


FIGURE 18. *Aethomylos simplicidens*, new genus and species, right lower molar, UCMP 101119; a. occlusal view, b. lingual view, c. labial view. Left P_{74} (DP_4), UCMP 101077; d. occlusal view, e. labial view, f. lingual view.

before making a nearly 90° lingual turn to contact the apex of the paraconid. The protoconid is higher than the metaconid and is situated farther anteriorly. As a result, the posterior margin of the trigonid is distinctively oblique in occlusal view. The talonid has a broadly excavated basin bordered by three cusps. The hypoconid is much higher than the hypoconulid. In UCMP 101625, the gently sloped lingual face of the hypoconid shows a sculpturing in the form of three or four faint, rounded other lower molar specimens. UCMP 101630, a probable M3, differs from all other referred lower molar specimens in having a relatively narrower talonid, a more bulbous hypoconid, and a more transversely compressed entoconid.

Remarks.—*Aethomylos simplicidens* may not be an insectivore at all; I can find no dental features in this species which indicate a close relationship with any of the presently recognized insectivore families.

Eocene apatemyids show a resemblance to *Aethomylos* in 1) the bowl-shaped structure of the talonid basin, 2) the angular anterolabial corner of the trigonid, 3) the low profile of the trigonids, 4) the forward slant of the posterior trigonid face, and

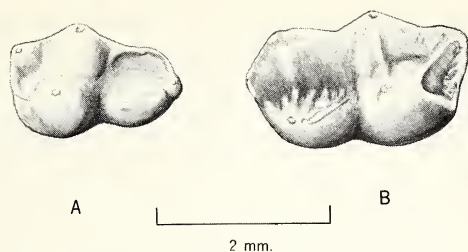


FIGURE 19. *Aethomylos simplicidens*, new genus and species, a. left lower molar (M_3), UCMP 101630; b. right lower molar (M_1 or M_2), UCMP 101625. All views occlusal.

5) the more posterior position of the metaconid relative to that of the protoconid. However, in Eocene apatemyids the anterolabial corner of the trigonid is actually farther forward than the apex of the paraconid, lending to the trigonid a characteristic parallelogram-like outline in occlusal view. No apatemyid known has a well-developed molariform P_4 ; instead, that tooth is quite reduced compared to M_1 . Upper teeth of Eocene apatemyids are poorly known, but most of the existing specimens (see McKenna 1963:34) are broadly different from the upper cheek teeth described above. The upper molar of *Labidolemur* (see West 1972), however, shows a resemblance.

The upper molars of certain oxyaenoid creodonts show a general resemblance to *Aethomylos* upper cheek teeth specimens (see *Oxyaena simpsoni*, Van Valen 1966:80, Plate 8, Figs. 1,2), but the metacone and the paracone are more closely appressed. Oxyaenoid lower molars differ from specimens referred to *Aethomylos* in a number of major features.

Although most members of the Didelphodontinae have transversely extended upper molars, in *Didelphodus altidens* Marsh (early-middle Eocene) and in *D. absarokae* Cope (early Eocene), these teeth are more transversely compressed and approach the equilateral-shaped outline of the upper molars of *Aethomylos*. Didelphodontines are also similar in the lack of a hypocone and lingual cingula, and in having conical paracones and metacones. Despite these superficial similarities, didelphodontine upper molars broadly contrast with those described above in their possession of a wide stylar shelf, a much closer approximation of the paracone and the metacone, both a paraconule and metaconule, and a smaller, less excavated protofossa.

The lower molars of *Didelphodus altidens* and *D. absarokae* show a similarity to the lower molars described here in the low profile of the trigonids, the forward slanting posterior trigonid face, and the talonid which is not sharply cornered. However, lower molars of these didelphodontine species do not show a sharply angular anterolabial corner of the trigonid and have relatively narrower talonids.

McKenna (1960a:88, Fig. 44a) described an isolated upper molar (UCMP 44772 D) from the Wasatchian Four Mile fauna which shows resemblance to the upper molars of *Aethomylos*. Unlike didelphodontines and like *Aethomylos*, UCMP 44772 D does not have a wide stylar shelf, and shows the presence of a broadly excavated protofossa. It differs from upper molars of *Aethomylos* in the possession of a reduced

paraconule and a weak mesostyle, characters which could conceivably be present in the structural ancestor of the San Diego genus.

It is obvious from the above comparison that no satisfactory assignment can be made for this new San Diego genus, but it serves as additional documentation of the remarkable diversity of insectivores in the San Diego region during the later Eocene.

TABLE 5
Measurements of the lower cheek teeth referred to
Aethomylos simplicidens

Element	Measurements	
P_4	<u>UCMP 96088</u>	<u>UCMP 101077</u>
length	1.82	2.24
trigonid width	0.76	0.81
talonid width	0.85	0.92
M_{1-2}	<u>UCMP 101119</u>	<u>UCMP 101625</u>
length	2.27	2.57
trigonid width	1.29	1.32
talonid width	1.25	1.31
	<u>UCMP 101645</u>	<u>UCMP 101750</u>
length	1.91	2.27
trigonid width	1.14	1.30
talonid width	1.48	1.32
M_3	<u>UCMP 101630</u>	
length	1.94	
trigonid width	1.25	
talonid width	0.92	

TABLE 6
Measurements of upper molars and premolars of
Aethomylos simplicidens

Specimen	Length	Anterior Width	Posterior Width
UCMP 96133 (type)	2.40	2.42	2.41
UCMP 96443	1.85	---	---
UCMP 99428	2.18	1.81	2.06
UCMP 101047	1.55	1.93	1.55
UCMP 101066	2.00	1.94	1.90
UCMP 101312	1.80	1.75	1.87
UCMP 101590	2.23	2.21	2.27
UCMP 104178	2.31	2.23	2.30

DISCUSSION AND CONCLUSIONS

Insectivora: faunal list.—The following insectivore taxa have been discovered from localities in the Friars and Mission Valley Formations and from UCMP locality V-72088 (unnamed formation) of San Diego County, California:

Class Mammalia
Subclass Theria
Infraclass Eutheria

Order Proteutheria

Family Apatemyidae
Subfamily Apatemyinae
cf. *Apatemys* sp. Marsh 1872

Family ?Palaeoryctidae
Subfamily ?Palaeoryctinae
Genus and species *indet.* probably new

Order Insectivora

Superfamily Erinaceoidea
Family Adapisoricidae
Sespedectes singularis Stock 1935
cf. *Proterixoides davis* Stock 1935
Cryptolestes vaughni n. gen. and sp.

Superfamily Soricoidae

Family Nyctitheriidae
Subfamily Nyctitheriinae
cf. *Nyctitherium* sp. Marsh 1872

Family Geolabididae

Subfamily Geolabidinae
Centetodon (= *Geolabis*) sp. Marsh 1872
Batodonoides powayensis n. gen. and sp.

Family ?Apternodontidea

Subfamily ?Apternodontinae
New genus and species unnamed

Order Insectivora *incertae sedis*

Erinaceoid-like genus and species
Micropternodontine-like genus and species
Aethomylos simplicidens n. gen. and sp.

Comparisons of the local insectivore fauna with those of other Eocene North American vertebrate localities are difficult because the results of recently intensified collecting in the latter areas are largely unpublished. However, at this early stage of research it is evident from the above taxonomic list that insectivores were well represented in the San Diego Uintan fauna. Such a diversity presently equals, if not exceeds, that of any other known North American later Eocene insectivore fauna except that of the Hendry Ranch Member, Badwater Creek localities, Wyoming, in which

thirteen insectivore taxa were recognized (Setoguchi 1973, unpublished Master's Thesis, Texas Tech. Univ.; and Black and Dawson 1966).

The scarcity of insectivore remains from later Eocene faunas other than the San Diego or Badwater-Hendry Ranch assemblages is probably a reflection of disparity in collecting technique rather than a reality. Of the localities listed by Black and Dawson (p. 334), only the San Diego and Badwater deposits have been subjected to intensive underwater screening operations (see McKenna 1965, for a description of this collecting procedure).

Age of the San Diego Insectivore Fauna—Insectivore genera which have ranges extending into the Oligocene and later times, such as *Domnina*, *Ankylo-don*, *Oligoryctes*, and *Apternodus*, are represented in the Badwater faunas but are absent from the San Diego fossil samples. This is not surprising because of the younger age assigned to the Badwater local fauna (see Black and Dawson 1966:344). *Centetodon* is the one San Diego genus that is known also from the North American Oligocene and earliest Miocene, but Lillegraven (*personal communication*) feels that the San Diego species of *Centetodon* are rather primitive forms closely related to Bridgerian species of that genus. Two insectivore taxa, cf. *Nyctitherium* and *Apatemys* sp., suggest a late Bridgerian-early Uintan age for the fauna. *Nyctitherium* is well represented in Bridgerian rocks, but Uintan fossils representing this genus are rare (see Robinson 1968; Black and Dawson 1966). However, such a poor Uintan record may be a function of both inadequate sampling and poor preservation of these diminutive forms. *Apatemys* sp. shows a close resemblance to *A. bellus*, known from both Bridgerian and Uintan faunas. *Sespedectes singularis*, *Proterixoides davis*i, and *Cryptolestes vaughni* are not known outside the southern California later Eocene, but I regard these genera as closely related to and not particularly advanced over Wasatchian and Bridgerian adapisoricids. Correlation is not yet possible using the remaining insectivore taxa from the San Diego fauna because of their aberrance or poor representation. However, the meager evidence available suggests a primitive aspect for the fauna. If the identification of UCMP 96081 as a possible palaeoryctine is correct, it marks a hitherto unknown Eocene distribution for this specialized late Paleocene subfamily. The possible apternodontine upper molar is of a more primitive structure than the late Eocene-Oligocene genera *Oligoryctes* and *Apternodus*. The upper and lower molars of *Aethomylos* are of primitive morphologies that are reminiscent of certain Paleocene and early Eocene mammals. Animals similar to *Batodonoides powayensis* would not be an unexpected discovery in a Late Cretaceous fauna; the species shows a striking resemblance to *Batodon tenuis* of that age. *B. powayensis* is certainly more primitive than any of the currently recognized species of *Centetodon*.

San Diego mammals on the whole seem more primitive than the Uintan forms of the Sespe region and the largely unstudied Laguna Riviera fauna from Carlsbad (located about forty-five miles north of San Diego). They appear, however, to be advanced over typical Bridgerian mammals from the North American Rocky Mountain region. Thus, an early Uintan age for the fauna is suggested. The fauna has traditionally been considered to represent "late Eocene" time (e.g., Black and

Dawson 1966). Acceptance of Steineck's and Gibson's (1971) arguments would, however, push back the age of the Uintan Mission Valley and Friars Formation mammalian faunas in correlation with the older time intervals represented by "Ulatisian" Ardath Shale and the "Narizian" Stadium Conglomerate foraminiferal faunas (Lillegraven 1973). Such an action would significantly broaden the concept of the Uintan to include some of the earlier half of the Eocene as well as most of the late Eocene. Consequently, the term "late Eocene" as applied to the San Diego Uintan vertebrate fauna would not be strictly appropriate. In acknowledgment of the possibility that the Uintan concept may eventually be broadened, the term "later Eocene" has been used throughout this paper in reference to the local fauna.

The primitive nature of the San Diego insectivores certainly does not conflict with a concept of an earliest Uintan age for the local fauna.

Geographical implication of the San Diego Insectivore Fauna.—A certain degree of endemism for the southern California Uintan fauna was suggested by Black and Dawson (1966). Despite the poor documentation of North American Eocene insectivores, there are strong indications that the San Diego insectivore fauna was highly endemic. Of the twelve insectivore taxa described from San Diego in this report, only *Apatemys*, *Nyctitherium*, and *Centetodon* are known elsewhere in the later Eocene of North America. Black and Dawson (1966:340) stated that the most widespread and best documented insectivore distribution is that of the family Leptictidae. Leptictids are conspicuously absent from the San Diego Uintan fauna. The evidence for this family in southern California faunas consists of a single fragmentary mandible specimen with M₃ (LACM (CIT) 1679, now lost) described by Stock (1935) from locality LACM (CIT) 150 in the Sespe Formation. I am not convinced that Stock's reference of that specimen to the Leptictidae is correct, as an illustration (Stock 1935:216, Fig. 5) of LACM 1679 shows some rather aberrant dental features. The M₃ of *Cryptolestes* shows resemblances to M₃'s of many leptictids and it is possible that Stock's specimen is referable to this rather abundant San Diego genus.

Most interesting is the fact that the ubiquitous and abundant southern California insectivore species *Sespedectes singularis* is known from nowhere else in North America. This form is usually found in such large numbers at a given locality that one would likewise expect to have found it by now in some of the midcontinental localities. The restriction of *Sespedectes singularis* and the closely related species, *Proterixoides davisii*, within southern California may be a reflection of a particular environment not represented in known samples from the more continental localities.

The remaining taxa from San Diego have not been found elsewhere in North America. They are also (with the possible exception of *Cryptolestes*) rather aberrant forms which are taxonomically enigmatic, even at the familial level.

I suspect that the seemingly unique nature of the San Diego insectivore fauna is in part due to monographic problems. However, one might venture an intriguing, though purely conjectural, interpretation that some of the insectivores in the San Diego fauna may be part of a more southern, perhaps Central American, radiation. Such a proposition does not seem so farfetched if one considers that southern California may have been opposite western Sonora in the later Eocene prior to significant

independent movement as part of the Pacific Plate on the west side of the San Andreas fault system (Minch 1972). This region would thus be much farther removed geographically from the midcontinental Rocky Mountain areas of the United States than it is today. There is no fossil evidence for early Tertiary insectivores in Central America, and there are only two insectivore (soricid) genera found in that region today. However, this does not preclude the possibility that insectivores once flourished in Central America. The present-day insectivore fauna of North America is hardly comparable with the vast diversity that existed there in the earlier Cenozoic.

NOTE ADDED IN PROOF

Since the submission of this paper for publication, several studies have been issued which relate to the later Eocene insectivore fauna from San Diego and warrant mention.

Lillegraven and Wilson (1975) tentatively referred the Camp Pendleton locality (UCMP loc. V-72088) to the Santiago formation (of Woodring and Popenoe, 1945), remarking on the lack of published geologic maps and descriptions of the district encompassing the locality. The views expressed above concerning the "local" and "distal" vertebrate associations represented at locality V-72088 are in agreement with Lillegraven and Wilson's (1975) analysis of the preservation of the rodent *Simimys* at that locality. These authors also noted the reoccurrent association of *Simimys* and *Sespedectes* in localities from Fletcher Hills, Camp Pendleton, and the Sespe Formation, and the interesting absence of these taxa in localities from Rancho de los peñasquitos (the Poway localities listed in Table 1 above). The unique faunal character of the latter region is thus underscored.

In an important review of European adapisoricids, Russell et al. (1975) subdivided the Adapisoricidae into the subfamilies Adapisoricinae (to include *Adapisorex*) and the Dormaalinae (to include *Litolestes*, *Leipsanolestes*, *Dormaalius*, *Entomolestes*, *Matronella*, "*Leptacodon*" *jepseni*, *Macrocraonion*, *Scenopagus*, *?Proterixoides*, *?Sespedectes*, *Talpavus*, and *Ankylodon*).

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A REVIEW OF THE GARTER SNAKE
THAMNOPHIS ELEGANS IN MEXICO



By ROBERT G. WEBB

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A REVIEW OF THE GARTER SNAKE *THAMNOPHIS ELEGANS* IN MEXICO¹

By ROBERT G. WEBB²

ABSTRACT: The little-known Mexican garter snake, *Thamnophis elegans errans* Smith is redescribed. Field work and an examination of most available specimens, including the type-material, provide data that amplify known variation and demonstrate intergradation with *T. elegans vagrans* in northwestern Chihuahua. *Thamnophis e. errans* occurs in pine-oak forests of the Sierra Madre Occidental and is known from the Mexican states of Chihuahua, Durango, and Zacatecas.

INTRODUCTION

I am aware of only four publications that provide noteworthy data concerning *Thamnophis elegans* in Mexico. In the original description, Smith (1942) presented morphological data on the type series of six specimens, and he referred to them as a subspecies of *ordinoides* (= *elegans*). Fitch (1948) reinterpreted Smith's data and considered *errans* to be a distinct species. Smith, et al. (1950), employing Fitch's nomenclature, commented on variation in eight specimens in the British Museum. Tanner (1959), in discussing new material from Chihuahua, treated *errans* as a subspecies of *elegans*. It is the purpose of this report to augment previous knowledge concerning variation and the distribution of *T. e. errans*, and to comment on intergradation with *T. elegans vagrans* in northern Chihuahua.

Specimens utilized are deposited in the following institutions (to which the abbreviations refer in the text): BYU, Brigham Young University; BMNH, British Museum (Natural History); FMNH, Field Museum of Natural History; KU, University of Kansas, Museum of Natural History; LACM, Natural History Museum of Los Angeles County; MSU, The Museum, Michigan State University; MVZ, Museum of Vertebrate Zoology, University of California; UAZ, University of Arizona, Department of Biological Sciences; UNM, University of New Mexico, Museum of Southwestern Biology; and USNM, National Museum of Natural History. I am grateful to the persons in charge of the above-mentioned collections;

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ROBERT L. BEZY

ROGER CONANT

DOUGLAS A. ROSSMAN

JOHN W. WRIGHT

²Research Associate in Herpetology, Natural History Museum of Los Angeles County, and Department of Biological Sciences, The University of Texas at El Paso, El Paso, Texas 79968.

Robert F. Inger and George R. Zug allowed me to borrow type material. I especially thank Rollin H. Baker for aid in the field on numerous occasions, Tom Van Devender and Michael D. Robinson for aid extended in my study of UAZ Chihuahuan specimens, and Richard C. Lovelace for the photograph of the holotype (Fig. 2).

THAMNOPHIS ELEGANS ERRANS SMITH
MEXICAN WANDERING GARTER SNAKE

Thamnophis ordinoides errans Smith 1942:112.

Thamnophis errans Fitch 1948:122.

Thamnophis elegans errans Tanner 1959:168.

Type Material: Holotype—USNM 46336, female, from near Colonia García, Chihuahua. Paratypes—Three topotypes, USNM 46337-39, and two from Coyotes, Durango, FMNH 1499 (2).

Diagnosis: The following combination of characters serves to distinguish *T. e. errans* from the annectent subspecies *T. e. vagrans*, as well as from all other species of garter snakes geographically sympatric with *T. e. errans*: Dorsal scale rows 19-19-17; supralabials 7; pale vertebral stripe distinct throughout length of body and tail and usually confined to vertebral row; pale lateral stripe on second and third scale rows anteriorly and only slightly paler than first dorsal row; black collar usually not separated middorsally by pale vertebral stripe; immaculate belly with pale orange wash (in life) in snakes (both sexes) exceeding 350 mm body length; tongue entirely black.

Thamnophis elegans errans is easily confused with *Thamnophis cyrtopsis*. Three specimens (MSU 560, 3167, 3677) considered to be *T. cyrtopsis* by Conant (1963:494), and another (KU 33871) referred to *T. cyrtopsis cyclides* by Chrapliwy and Fugler (1955:127) are *T. e. errans*. *Thamnophis e. errans* and *T. cyrtopsis* resemble each other in having 19-19-17 dorsal scale rows, and the pale lateral stripe on the second and third dorsal scale rows. The sympatric subspecies *T. cyrtopsis pulchrilatus* further resembles *T. e. errans* in having seven supralabials and the vertebral stripe confined to the vertebral row. These two forms can be distinguished by a difference in overall coloration. The dorsolateral area is olive in *T. e. errans*, and black in *T. c. pulchrilatus*; the first dorsal scale row is scarcely darker than the pale lateral stripe in *T. e. errans*, but is blackish brown in *T. c. pulchrilatus*. *Thamnophis e. errans* is distinguished from all subspecies of *T. cyrtopsis* by having the tongue entirely black (instead of red with black tip) and the venter pale orange (instead of yellow) in adults. Both of these color characteristics are difficult, if not impossible, to determine in preserved material.

DESCRIPTION

Color and Pattern: Top of head dark brown to olive brown; parietal spots absent or obscure; black nuchal blotch or collar about five scales long, extending laterally to third or fourth dorsal scale row; anterior part of black collar (small dorsal

scales behind parietals) often brown; black collar occasionally interrupted by vertebral stripe, but usually complete and indented posteriorly where vertebral stripe terminates; yellow or buff vertebral stripe distinct throughout length of body and tail, but sometimes dim posteriorly; vertebral stripe confined to vertebral row, occasionally covering parts of adjacent scale rows, and usually slightly expanded and bright yellow just behind black collar; black marks on sutures between supralabials, if present, usually not reaching edge of lip with exception of posteriormost black mark; black marks lacking on infralabial sutures, except for suture between ninth and tenth infralabials; dorsolateral area uniformly gray-green or olive, or with indistinct black spots arranged in checkerboard fashion, the uppermost spots encroaching on vertebral stripe; checkerboard pattern occasionally evident throughout length of body; largest black spots in dorsolateral areas on neck; checkerboard pattern more evident anteriorly than posteriorly and more so in young than in adults; scattered white flecks in dorsolateral areas in some specimens; keels of scales in dorsolateral areas slightly paler than ground color; pale lateral stripe on second and third dorsal scale rows only slightly paler than first dorsal scale row; edges of some scales of first three dorsal scale rows often black; black spots occasional on first scale row in neck region; belly immaculate pale yellow in young but pale orange in specimens exceeding 350 mm SVL; tongue entirely black.

Notes on color and pattern of living snakes are as follows: Six new-born young (LACM 116064-69, SVL 175 to 188 mm)—top of head dark brown with indistinct parietal spots; collar black with yellow dots immediately behind parietals; vertebral stripe yellow-green; dorsolateral area olive with black spotting anteriorly but becoming patternless posteriorly; lateral stripe olive-yellow, only slightly paler than first dorsal scale row; underside of head white; belly and underside of tail pale yellow. Adult male (LACM 116073, SVL 526 mm)—top of head brown blending posteriorly with black collar; vertebral stripe white-yellow; dorsolateral area brown-olive with black specks anteriorly; lateral stripe cream; first scale row gray-green with orange tinge; underside of head and neck white with yellow-orange tinge; belly and underside of tail orange; iris buff with brown marks. Adult female (LACM 116079, SVL 536 mm, Fig. 1)—top of head and dorsolateral area dark olive; nuchal blotch black; scattered black specks in dorsolateral area; vertebral and lateral stripes yellow; first scale row and adjacent part of ventrals pale olive; supralabials yellow with lower part of supralabials three to six pale orange; underside of head pale yellow with ventrolateral part pale orange; belly and underside of tail pale orange; iris pale orange with brown marks.

A small male (LACM 116077, SVL 187 mm) has the third, fourth, and fifth supralabials pale orange, a small pale orange blotch at the angle of the jaw under the seventh supralabial, the underside of the head white, and the rest of the ventral surface including the tail yellow-green. A male of larger size (LACM 116078, SVL 343 mm) resembles the above-mentioned female except that the orange is brighter on the lower parts of the supralabials and anteriorly on the belly; the underside of the tail is green-yellow with only a faint pale orange tinge.

The tongue in all specimens is slaty gray. The pale orange ventral color, observed only in living specimens, shows ontogenetic development, appearing first



FIGURE 1. Top, pine-oak forest, general habitat of *Thamnophis elegans errans*, 15 km. NW Valparaiso, 2545 m, Zacatecas. Bottom, adult female (LACM 116079, SVL 536 mm) from above locality. Both photographs taken 31 July 1970.

on the sides of the head, then encroaching on the belly, and finally the underside of the tail. Snakes exceeding 300 mm show some pale orange on the ventral surfaces; seemingly all specimens (both sexes) that exceed 350 mm SVL have the entire ventral surface pale orange (except underside of head).

Scutellation: Emphasis was placed on the number of dorsal scale rows, supralabials, ventrals and caudals (subcaudals). All specimens have the dorsal scales in 19-19-17 rows. Seven supralabials (third and fourth entering orbit) occur most frequently (97%). The posterior supralabials (especially the sixth and seventh) are enlarged; the sixth is higher than long. Ventrals in 24 males average 157.5 (150 to 164), and in 20 females, 151.9 (146 to 159). Caudal scales in 23 males average 86.4 (78 to 93), and in 16 females, 74.6 (69 to 81). These data on scutellation exclude specimens from the area of intergradation in northwestern Chihuahua; for a further discussion see section on intergradation and Tables 1 and 2.

Variation in ventral and caudal scales in two broods of young is available. A female (KU 40338, obtained on 25 June, SVL 450 mm) has 152 ventrals and 73 caudals and it contained eight well-developed young. One of the young (KU 40343), about 90 mm SVL, is deformed in having the first supralabials missing (cleft upper

TABLE 1

Variation in number of dorsal scale rows, supralabials, and ventral pattern of New Mexico sample of *T. e. vagrans*, of three largest Chihuahuan samples of intergrades, and of *T. e. errans*.

Sample	Dorsal Scale-Rows		Supralabials		Ventral Pattern	
<i>T. e. vagrans</i> New Mexico	19-19-17	0 (0%)	7-7	0 (0%)	1 21	(40%)
	21-19-17	7 (13%)	7-8	3 (6%)	2 19	(36%)
	21-21-17	45 (85%)	8-8	51 (94%)	3 13	(24%)
	23-21-17	1 (2%)				
Intergrades Chuhuichupa	19-19-17	8 (30%)	7-7	14 (52%)	1 13	(48%)
	19-21-17	2 (7%)	7-8	6 (22%)	2 10	(37%)
	21-19-17	12 (44%)	8-8	7 (26%)	3 4	(15%)
	21-21-17	5 (19%)				
Intergrades Yepómera	19-19-17	0 (0%)	6-7	1 (5%)	1 0	(0%)
	19-21-17	1 (5%)	7-7	9 (45%)	2 7	(35%)
	21-19-17	14 (70%)	7-8	5 (25%)	3 13	(65%)
	21-19-15	1 (5%)	8-8	5 (25%)		
	21-21-17	4 (20%)				
Intergrades Santa Clara	19-19-17	0 (0%)	7-7	2 (20%)	1 0	(0%)
	19-21-17	1 (10%)	7-8	2 (20%)	2 5	(50%)
	21-19-17	4 (40%)	8-8	6 (60%)	3 5	(50%)
	21-21-17	5 (50%)				
<i>T. e. errans</i> S Chihuahua and southward	19-19-17	56 (100%)	6-8	1 (2%)	1 56	(100%)
			7-7	53 (96%)		
			7-8	1 (2%)		
			8-8	0 (0%)		

TABLE 2

Variation in number of ventral and caudal scales of New Mexico sample of *Thamnophis elegans vagrans*, of intergrades, and of *T. e. errans*.

Sample	Ventrals			Caudals		
	N	Range	Mean	N	Range	Mean
<i>T. e. vagrans</i>						
New Mexico						
Males	22	155-171	160.0	19	75-94	83.5
Females	32	147-160	153.0	30	70-87	75.2
Intergrades						
NW Chihuahua						
Males	25	153-166	160.5	19	78-94	83.9
Females	21	147-160	153.6	16	67-83	73.6
<i>T. e. errans</i>						
S Chihuahua and southward						
Males	24	150-164	157.5	23	78-93	86.4
Females	20	146-159	151.9	16	69-81	74.6

lips) and many incomplete, partial ventral scales. Data for the seven other unsexed young are: average SVL, 132.6 (124 to 138), and average tail length, 51.3 (43 to 71) mm; average number of ventrals, 155.4 (151 to 160), and of caudals, 85.7 (74 to 92); and, average position of umbilical scar on ventral 133.9 (131 to 137). For six young born on 28 July (not measured until 20 August) to a female (LACM 116063, SVL 472 mm) that has 155 ventrals and 79 caudals, the data are: average SVL, 182.5 (175 to 188) and of tail, 64.6 (61 to 70) mm; number of ventrals 153, 156, and 159, and caudals 89, 90, and 91, respectively, in three males; number of ventrals 153, 153, and 156, and caudals 76, 77, and 81, respectively, in three females; and, position of umbilical scar on ventral 136, 137, and 141 in three males, and on ventral 133, 134, and 135 in three females.

There is broad contact of the internasals with the rostral; the ratio of internasorostral to nasorostral contact averages 1.50 (1.2 to 1.9). The average ratio of the lengths of anterior to posterior chin shields is 0.85 (0.7 to 1.2); these characters are discussed further in the section on intergradation. Maxillary teeth range from 16 to 19 in *T. e. errans* (Smith, 1942; Smith, et al., 1950; Tanner, 1959).

Types: The holotype (Fig. 2) and three paratopotypes (USNM 46336-39) are from near Colonia García in northwestern Chihuahua, which is in an area where intergradation occurs with *T. e. vagrans*. The four specimens most closely resemble *T. e. errans*, but influences of *T. e. vagrans* include the blackened anterior edges of many ventral scales in USNM 46337; eight supralabials (right side of head) in USNM 46339; and black flecking posteriorly and laterally on the belly and eight supralabials on one side of the head in the holotype (USNM 46336). The two paratypes from Coyotes, Durango (both cataloged FMNH 1499), are referable to *T. e.*



FIGURE 2. Holotype of *Thamnophis elegans errans*, USNM 46336, from near Colonia García, Chihuahua. Photograph by Richard C. Lovelace.

errans; they were collected by Heller and Barber in August, 1904. The larger of the two specimens is unusual in having a wide vertebral stripe (covering halves of adjacent paravertebral rows), a few dark flecks posteriorly and midventrally on the belly, and in having the dark collar narrowly interrupted by the vertebral stripe. The smaller specimen from Coyotes has the anteriormost pair of large dark body blotches confluent middorsally. Other data were provided by Smith (1942) in the original description.

INTERGRADATION WITH *THAMNOPHIS ELEGANS VAGRANS*

Tanner (1959) studied snakes from the northernmost part of the range near the type locality of *T. e. errans* (northwestern Chihuahua) that shared characteristics with *T. e. vagrans* (21 dorsal scale rows and 8 supralabials). He considered this variation to be representative of *T. e. errans*. Tanner, however, was unaware of the invariable occurrence of 19 scale rows and 7 supralabials in populations of *T. e. errans* to the south. Twenty-one scale rows, eight supralabials, and a black mid-ventral pattern are characteristic of *T. e. vagrans*, which occurs northward into Arizona, New Mexico, and beyond. Because these three features occur in some specimens [of *T. e. errans*] from northwestern Chihuahua and are absent in *T. e. errans* elsewhere, the specimens from northwestern Chihuahua are considered to reflect intergradation with *T. e. vagrans*.

Thamnophis e. errans has a maximum of 19 dorsal scale rows (100%) and seven supralabials (97%). The ventral surface is immaculate pale yellow or orange. In some specimens (LACM 116072, 116074) close examination reveals some ventral scales with the anteriolateral edges narrowly blackened, and a young specimen (LACM 116070) has tiny black dots arranged in a short midventral row posteriorly. The diagnostic characteristics for *T. e. errans* (maximum of 19 scale rows and 7 supralabials, and lack of black ventrally) occur occasionally in *T. e. vagrans* according to the detailed studies of Van Denburgh and Slevin (1917, data reiterated by Van Denburgh, 1922) and Fitch (1940). Tanner (1959) also reported data on scutellation for *T. e. vagrans*.

Fifty-four specimens of *T. e. vagrans* from the vicinity of Glenwood and Mogollon in southwestern Catron County, New Mexico were examined for comparative purposes. Most of these have 21-21-17 dorsal scale rows (85%); less frequent combinations are 21-19-17 (13%) and 23-21-17 (2%). Eight supralabials (fourth and fifth entering orbit) occur most frequently (97%). The number-coded ventral patterns (explained in next paragraph) of 1 (40%) and 2 (36%) are more frequent than the extensive black belly pattern of 3 (24%); the average number-coded ventral pattern for this New Mexico population is 1.85. Ventrals in 22 males average 160.0 (155 to 171), and in 32 females, 153.0 (147 to 160). Caudals in 19 males average 83.5 (75 to 94), and in 30 females, 75.2 (70 to 87).

In specimens of *T. e. errans* from northwestern Chihuahua three characteristics—numbers of dorsal scale rows and supralabials, and ventral pattern—were used to assess intergradation between the subspecies *errans* and *vagrans*. The degree of black ventral pigmentation was number-coded as follows: 1—immaculate

or nearly so, 2—black pigmentation moderate, either confined to lateral spots on ends of ventrals (Fig. 28 in Stebbins 1966), or confined to scattered midventral spots or flecks, or a combination thereof, and 3—extensive black markings posteriorly, mostly continuous midventrally (Pl. 10 in Van Denburgh and Slevin 1917; Pl. 89 same in Van Denburgh 1922).

The specimens from this intergrading area are discussed by locality (1 to 8) below; the eight localities correspond to the north (1) to south (8) arrangement of the symbols on the distribution map (Fig. 3). The northernmost and southernmost localities—24 miles northeast Colonia García and Yepómera, respectively—are about 150 km apart.

1. 24 miles northeast Colonia García: one specimen; 21-21-17 scale rows, 7-7 supralabials, ventral pattern 2.
2. Colonia García: four specimens (holotype and paratypes); 19-19-17 scale rows in all; 7-8 supralabials in holotype and one paratype, others 7-7; ventral pattern 2 in holotype and one paratype, others 1.
3. 10.5 miles northeast El Largo: two specimens; both referable to *T. e. errans* in all features.
4. Colonia Chuhuichupa: 27 specimens (localities—Chuhuichupa, Black Canyon, and El Norte; see list of specimens); see Table 1.
5. Sierra del Nido: 2 specimens; both referable to *T. e. errans* in all features.
6. Santa Clara: 10 specimens; see Table 1.
7. 2 miles southwest San José Babícora: two specimens; both referable to *T. e. errans* in all features.
8. Yepómera: 20 specimens (localities—Yepómera and 5-6 kilometers north Yepómera); see Table 1.

The variation in the three largest samples (Chuhuichupa, Santa Clara, and Yepómera), as well as in *T. e. errans* (southern Chihuahua and southward) and in the New Mexico sample of *T. e. vagrans* is compared in Table 1. The Chuhuichupa sample is most like *T. e. errans*, the Yepómera sample is intermediate tending towards *T. e. vagrans*, and the Santa Clara sample is most like *T. e. vagrans*. In snakes with 21 rows anteriorly, 19 rows occur for a short distance just posterior to the neck and 21 rows extend posteriorly to near midbody. Many snakes in the Yepómera and Santa Clara samples have wide middorsal stripes that occupy the vertebral row and halves of the adjacent rows. The black ventral pigmentation is most extensive in specimens (especially MVZ 73074, 73076) from the Santa Clara sample. It is of interest that the specimens comprising the Yepómera sample are from a lower elevation (1890 m) in a general grassland habitat (Van Devender, 1973) rather than in pine-oak forest; the ten snakes from the vicinity of Santa Clara are also from a correspondingly low elevation (1860 to 1890 m).

Of interest is the variation within a single brood of 10 young (UAZ 34889-98, born 10 July). The female (UAZ 34888, obtained 18 June at Yepómera, SVL 461 mm) has 21-21-17 scale rows, 7-7 supralabials, a type 2 ventral pattern (approaching type 3), 156 ventrals and 72 caudals. Data for the 10 young are: average SVL 151.0 (143 to 155) mm (date measured unknown); average number of ventrals 154.6

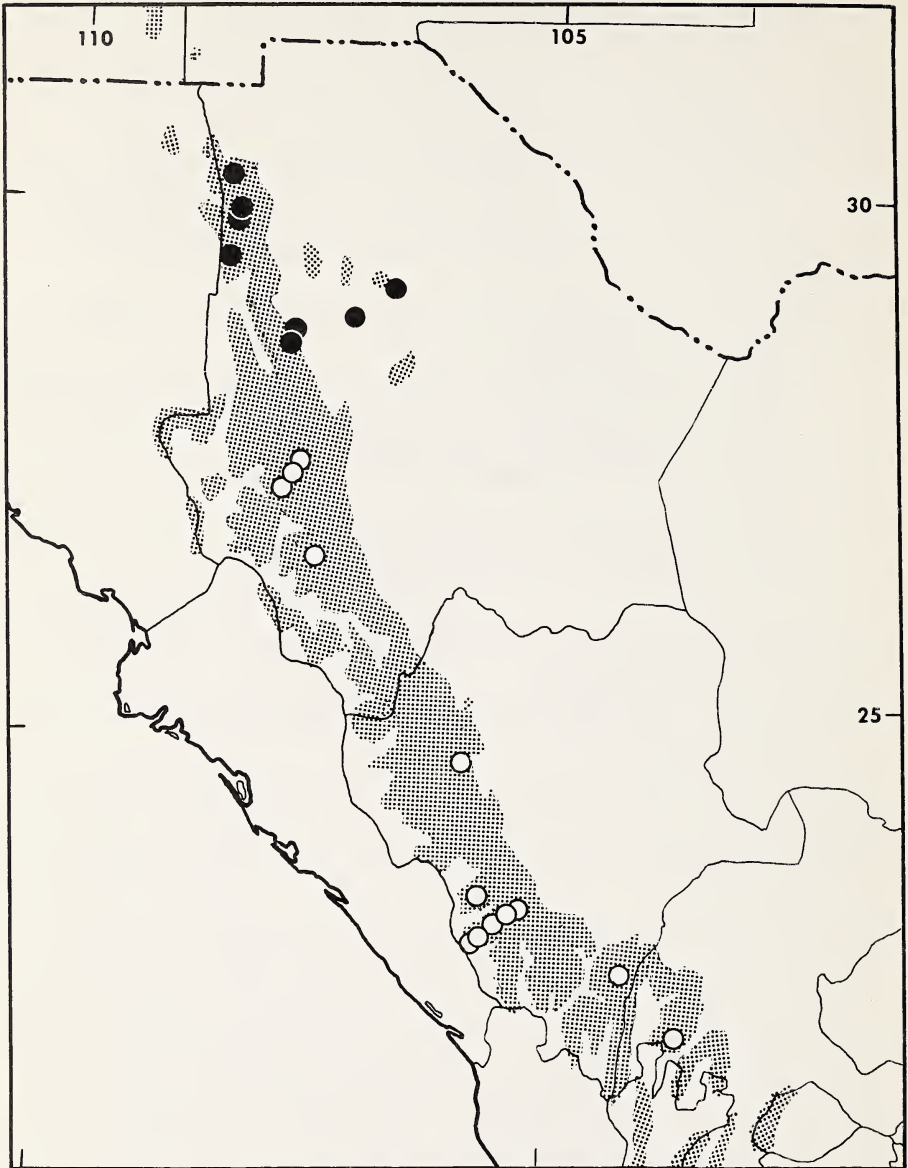


FIGURE 3. Map of northwestern Mexico showing localities (open circles) for *Thamnophis elegans errans*; localities representing intergrading population with *T. e. vagrans* in northwestern Chihuahua indicated by solid circles. Localities a short distance apart share the same symbol. Shaded area indicates approximate extent of pine-oak forest in Sierra Madre Occidental.

(151 to 160) and caudals 78.5 (70 to 85); dorsal scale rows 21-19-17 in eight, 21-21-17 in one, and 19-21-17 in one; supralabials 7-7 in two, 7-8 in four, and 8-8 in four; and, an average coded ventral pattern of 2.7 (2 to 3).

The maximum number of scale rows and supralabials are the most meaningful of the three characteristics used to assess intergradation. Specimens that otherwise have evidence of intergradation resemble *T. e. errans* in features of color and pattern. Some specimens lack evidence of intergradation and are indistinguishable from *T. e. errans*. Tongue color has not been observed in live snakes from the intergrading area, but further resemblance to *T. e. errans* is indicated by the completely black tongue of one recently preserved snake (LACM 75431). The tongue is red, black-tipped in live specimens of *T. e. vagrans* from the Sacramento Mountains, Otero County, and from near Black Mountain, Catron County, New Mexico. The exposed tongue of some preserved specimens of *T. e. vagrans* (UNM) is also pale (red) with a black tip.

Variation in numbers of ventral and caudal scales of both sexes is noted in Table 2 for *T. e. errans* (southern Chihuahua and southward), for [*T. e. errans* from the intergrading area with *T. e. vagrans*] northwestern Chihuahua, and for the New Mexico population of *T. e. vagrans*. Ventral scales were counted according to the Dowling method (1951). Males have more ventral and caudal scales than females of both subspecies. Geographic variation seems to be negligible, with little difference in either sex in numbers of ventral and caudal scales between the two subspecies. Data in Van Denburgh and Slevin (1917:242), Van Denburgh (1922:832), and Fitch (1940:11, Fig. 3) suggest geographic variation in numbers of ventral scales in the wide-ranging *T. e. vagrans*, and greater numbers of ventrals in both sexes elsewhere than that for the sample of *T. e. vagrans* examined from Catron County, New Mexico.

Two features of scutellation used to delineate subspecies in the *elegans* rasenkreis have been the relative lengths of the anterior and posterior pair of genials or chin shields (Fitch, 1940) and the shape of the internasals (Fitch, 1940; Fox, 1951). These characters were assessed only in the late stages of this study and values were determined for only a few specimens. The data for *T. e. errans* are compared below with corresponding data for *T. e. vagrans* provided by Fitch (1940), who explained the use of these characters.

The average ratio of internasorostral contact to nasorostral contact was given for *T. e. vagrans* from different localities by Fitch (1940:117, Table 10). It is of interest that the broadest, most truncate internasals (broadest contact with rostral) occur in the southernmost population from New Mexico and Arizona, averaging 1.12. In 16 *T. e. errans*, the internasorostral contact is broader, averaging 1.50 (1.2 to 1.9). In five snakes from the intergrading area in northern Chihuahua the degree of contact is about the same as in *T. e. errans* from farther south, averaging 1.48 (1.4 to 1.7). The relatively broader contact of the internasals and rostrals may further serve to distinguish *T. e. errans* from *T. e. vagrans*.

The average ratio of length of anterior chin shields to length of posterior chin shields was given for *T. e. vagrans* from different localities by Fitch (1940:119, Table 11). The average value of 0.94 for the New Mexico-Arizona population is about the

same as that for the five Chihuahuan snakes from the intergrading area (0.95, 0.8 to 1.2). In 16 *T. e. errans* the anterior chin shields average 85 per cent as long as the posterior pair (0.85, 0.7 to 1.2). However to judge from the values from throughout the range of *T. e. vagrans*, the relative lengths of the pairs of chin shields do not seem to differ appreciably in the two subspecies.

DISTRIBUTION

Thamnophis elegans errans is confined to the pine-oak forests of the Sierra Madre Occidental, at elevations exceeding about 2286 m, and is known from the Mexican states of Chihuahua, Durango, and Zacatecas (Fig. 3). Individuals seem not to frequent ponds and streams; they are often found away from the vicinity of water in damp or even dry places under cover of logs and rocks. The specimens examined are listed geographically from north to south by state and locality.

Specimens examined: Thamnophis elegans vagrans (54)—Catron County, New Mexico: State Fish Hatchery, Glenwood (UNM 4467-77, 5325, 5443-47, 6792, 10507-08, 11109, 11194-95, 11201); Willow Creek, T1N-R17W (UNM 8296); Willow Creek at Ranger Station (UNM 25698-99); Willow Creek, 10 mi. E Mogollon (UNM 4531-52, 4611-15). *Thamnophis elegans errans* x *T. e. vagrans* (68)—Chihuahua: 24 mi. NE Colonia García (LACM 75429); Colonia García (USNM 46336-39); 10.5 mi. NE El Largo (LACM 75430-31); Black Canyon, 8 mi. W Colonia Chuhuichupa (BYU 14225); El Norte, 3 mi. N Colonia Chuhuichupa (UAZ 35238, 35250-54); Colonia Chuhuichupa (BYU 13889-95, 13921-23, 14479-81, 14493-95, 14501, 14505, 15721, 15776); Arroyo Mesteño, Sierra del Nido (MVZ 73088, 73091); 2 mi. S Santa Clara (MVZ 70968); 1 mi. S and 0.5 mi. E Santa Clara (MVZ 73073-81); 2 mi. SW San José Babicora (KU 47315-16); Arroyo del Huachin, 5-6 km. N Yepómera (UAZ 34132-33, 34154-55); Yepómera (UAZ 34120, 34129-31, 34210, 34888-98). *Thamnophis elegans errans* (56)—Chihuahua: Bocoyna (BYU 15742); 2 mi. S Creel (BYU 14381, 14511, 15644, 17076-77); 15 mi. S and 16 mi. E Creel (KU 44286); Yoquiva (BMNH 1911.12.12.20); no data (LACM 21067). Durango: 18 mi. SSW Tepehuanes (LACM 116060-69); 1.5 mi. W San Luis (MSU 565); Hacienda Coyotes (FMNH 1499, N = 2; LACM 104092, 116070-75); 2 mi. NE El Salto (MVZ 67425); 6 mi. SW El Salto (LACM 116076); 10 mi. SW El Salto (KU 40338-46); 7 mi. SW Las Adjuntas (KU 33871); La Ciudad (BMNH 1882.11.15.22-25, 1882.11.15.27-29); 1 mi. SW La Ciudad (MSU 3167); 2.2 mi. W La Ciudad (LACM 50877); 1 mi. W Buenos Aires (LACM 104091); Rancho Las Margaritas (= El Capulin), ca. 22 km. SSE Mezquital (MSU 560, 3677). Zacatecas: 9 mi. NW Valparaiso (LACM 116077-79).

RESUMEN

Se redescubre la culebra *Thamnophis elegans errans* Smith y se demuestra su intergradación con *T. e. vagrans* en el noroeste de Chihuahua. *Thamnophis e. errans* está restringida a los bosques pino-encina de la Sierra Madre Occidental en los estados Mexicanos de Chihuahua, Durango y Zacatecas.

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THE ISLAND AND COASTAL VEGETATION AND FLORA OF THE
NORTHERN PART OF THE GULF OF CALIFORNIA

By RICHARD S. FELGER AND CHARLES H. LOWE

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THE ISLAND AND COASTAL VEGETATION AND FLORA OF THE NORTHERN PART OF THE GULF OF CALIFORNIA¹

By RICHARD S. FELGER² AND CHARLES H. LOWE³

ABSTRACT: The flora and vegetation of the eight major islands on the eastern (Sonoran) side of the Gulf of California are summarized, with comments on the coastal vegetation of Sonora and the gulf coast of Baja California. In order of decreasing size, the islands treated are Islas Tiburón, San Esteban, San Pedro Nolasco, San Pedro Mártir, Dátil (=Turners), Alcatraz, Patos, and Cholludo. The major plant communities are classified and characterized. These are: *Seagrass Meadow*, *Litoral Scrub* (mangrove scrub and salt scrub), *Desertscrub* (coast scrub, creosotebush scrub, mixed desertscrub, cactus scrub, riparian desertscrub, and riparian *aguajes* or *tinajas*), and *Thornscrub* (plains thornscrub, foothill thornscrub, and riparian thornscrub).

Three major disjunct thornscrub regions occur at higher elevations towards the southern part of the Sonoran Desert: (1) on Sierra de la Giganta, Baja California Sur, (2) the mountains northwest of Guaymas, Sonora, and (3) on Sierra Kunkaak, Isla Tiburón. Shreve's *Foothills of Sonora* subdivision of the Sonoran Desert is reclassified as thornscrub rather than desertscrub.

Checklists given for vascular plants on each of the eight islands are expected to be nearly complete except for Isla Tiburón, for which we estimate about 85 to 90 percent of the flora is known to us. The numbers of species for the islands are 286 on Tiburón, 107 on San Esteban, 55 on San Pedro Nolasco, 23 on San Pedro Mártir, 99 on Dátil, 43 on Alcatraz, 10 on Patos, and 28 on Cholludo. A ninth island, Isla San Jorge, is without vegetation.

Islands on the eastern side of the Gulf of California show stronger floristic relationships with Baja California than do the islands on the western side of the Gulf with the Sonoran mainland. Seven species, or 2.1 percent of the flora of the eight Sonoran islands, are endemic to one or more islands in the Gulf. In this island series single-island endemics occur only on Isla San Pedro Nolasco. There are no known endemic plants on Isla Tiburón, largest island in the Gulf of California.

Within the overall positive relationship of number of species to island area there is considerable variation among the smaller islands. Island size, isolation, topographic and habitat diversity, aridity, absence or presence of vertebrate herbivores, and guano deposits seem to be major factors influencing the evolution and distribution of the flora and vegetation of the islands in the Gulf of California.

Only 4 non-native plant species have become established on these islands, indicating that the agency of man, both ancient and modern, has had minimal impact on the natural biota. This is a rare situation for our times; protection of the natural ecosystems on the islands in the Gulf of California would be of great value for the future.

¹REVIEW COMMITTEE FOR THIS CONTRIBUTION

CHRISTOPHER DAVIDSON

WILLIAM MARTIN

ROBERT F. THORNE

²Arizona-Sonora Desert Museum, P.O. Box 5607, Tucson, AZ 85703.

³Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85719.

INTRODUCTION

In this report we discuss the vegetation of the islands in the northern part of the Gulf of California and of the adjacent coastline of mainland Sonora and peninsular Baja California, and summarize the flora and vegetation of the eight major islands of the east side of the Gulf of California. In order of decreasing size, the islands are Tiburón, San Esteban, San Pedro Nolasco, San Pedro Mártir, Dátil, Alcatraz, Patos, and Cholludo (Fig. 1). A ninth island, Isla San Jorge near the head of the Gulf, is without vegetation. This report is based on our investigations in northwestern Mexico during the past two decades.

Principal modern works dealing with the vegetation and flora of the Gulf of California region are Johnston (1924), Gentry (1949), Shreve (1951), Wiggins (1964), Felger (1966), and Hastings et al. (1972). Johnston (1924) and Lindsay (1955) provide excellent accounts of botanical explorations in the region, and biological investigations in Sonora and the adjacent islands are reviewed by Felger (1976-a).

Various systematic treatments encompassing diverse taxa in the region have appeared since publication of the *Flora of the Sonoran Desert* (Wiggins 1964), and nomenclatural changes resulting from these works are generally reflected in the comprehensive floristic listing given for each island in Table 1. (See pp. 33-53). Nomenclature given here represents our interpretation of the literature and specimens which we have studied. Many new records for the islands are reported in this paper. Several of the new records are based on populations discovered by Reid Moran of the San Diego Museum of Natural History, who has made extensive collections on the Gulf Islands.

There is a need for many taxonomic new combinations to reduce the number of artificial genera, species, and trinomials in the flora (Felger and Lowe 1970). With notable exception of such apomictic plants as *Opuntia fulgida*, we confine recognition of taxa below the species level to geographic races. Thus the distinction of variety versus subspecies is semantic rather than biosystematic.

VEGETATION OF THE NORTHERN GULF OF CALIFORNIA

Most of the geographic region treated here lies within the Sonoran Desert subdivision of the North American Desert (Shreve 1942, 1951). We also discuss the northernmost reaches of the semi-arid subtropical scrub (i.e., thornscrub) in western North America, which occurs at the southern margins of the Sonoran Desert. The flora is organized into several natural sets of distinctive communities, with life-forms and phytosociological relations similar to those of other subtropical and maritime ecosystems in arid and semi-arid regions of the world. Many of the terrestrial plant species and genera are peculiar to the North American Southwest, and specifically to the Pacific Subtropical West. Numerous others are shared between the Americas (see Johnston 1940; Solbrig 1972). The communities are natural

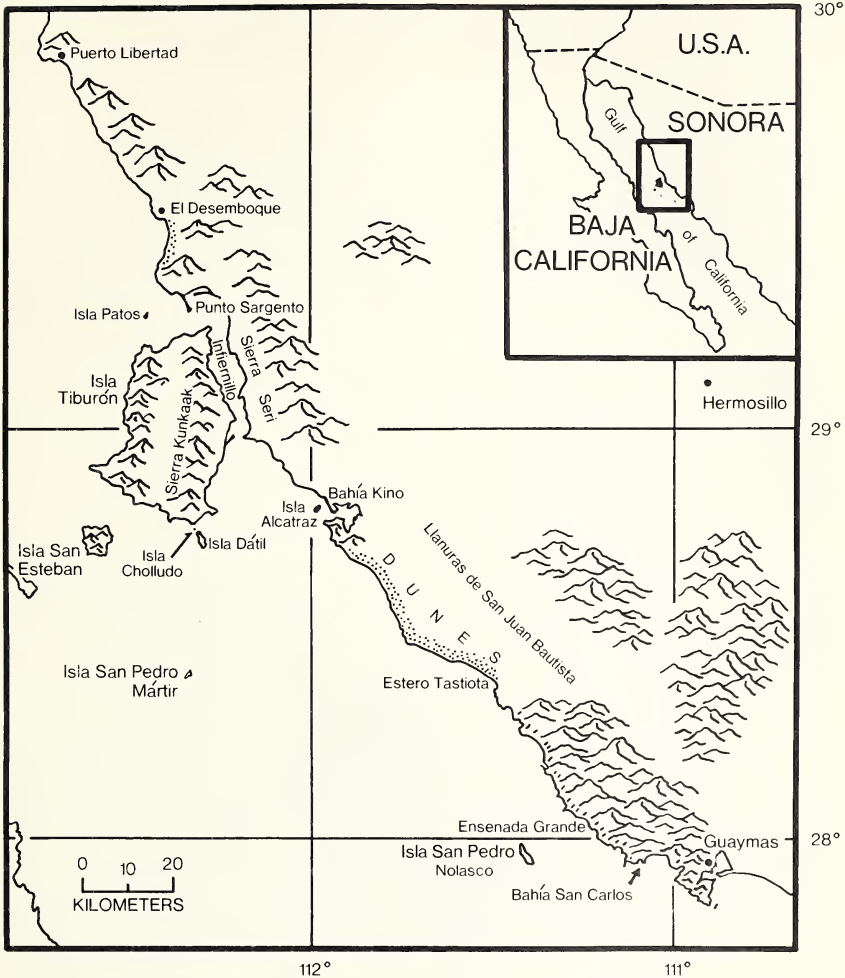


FIGURE 1. Central Gulf Coast of Sonora, and islands on the eastern side of the Gulf of California, Mexico.

biotic ones, but here, as elsewhere, the animals generally provide less critical information than do the plants for community delineation.

We find great variation in the community diversity in this region, which we attribute to the highly complex topography and correspondingly complex array of microenvironments. The major biotic communities are distributed as mosaics within a broader continuum from the littoral scrub of the tidelands across a highly varied desertscrub into the limited thornscrub of the better watered regions at higher elevations. The seagrass meadows are sharply differentiated from the adjacent tideland

vegetation and their microenvironmental distributions do not overlap. The major biotic communities of the northern part of the Gulf of California region are:

Seagrass Meadow

Littoral Scrub

mangrove scrub

salt scrub

Desertscrub

coast scrub

creosotebush scrub

mixed desertscrub

cactus scrub

riparian desertscrub

riparian *aguajes* (or *tinajas*)

Thornscrub

plains thornscrub

foothill thornscrub

riparian thornscrub

Short-tree Forest

(not in geographic area treated here).

The terrestrial vegetation of the northern Gulf region is Arid Subtropical Scrub (*sensu* Axelrod 1950, and elsewhere); it is an arid and semi-arid, predominantly drought-deciduous, subtropical scrub. Higher categories for the major communities listed in the foregoing are:

Seagrass Meadow

Subtropical Scrub

Littoral Scrub

mangrove scrub and salt scrub communities

Arid Subtropical Scrub

desertscrub communities

Semi-arid Subtropical Scrub

thornscrub and short-tree forest communities.

THE MAJOR COMMUNITIES

1. *Seagrass Meadow*.—Protected waters of the Gulf of California with muddy-sandy substrates at lower limits of subtidal zones, but mostly subtidal benthic zones to approximately 3 fathoms, and occasionally to approximately 5 fathoms: *Ruppia maritima* and *Zostera marina*. Northward about to the limits of the mangroves, with the most extensive seagrass meadows in the Canal del Infiernillo. For example, both species known from Bahía de Guaymas, Bacochibampo, and San Carlos, Estero Tastiota, and Canal del Infiernillo; *Zostera* from Bahía de la Concepción, several localities southward along the mainland to Altata, Sinaloa, and along the west coast of Baja California southward to Bahía Magdalena; and *Ruppia* from Bahía de la Paz (see Johnston 1924; den Hartog 1970; Felger and Moser 1973; and Felger and McRoy 1975).

2. *Littoral Scrub*.—Tidally inundated low scrub, halophytic vegetation, almost entirely evergreen and perennial, with predominance of succulent and semi-succulent species.

mangrove scrub

The mangroves: *Avicennia germinans*, *Laguncularia racemosa*, *Rhizophora mangle* (Fig. 2). Quiet bays, and lagoons locally called *esteros*. In Sonora north to the estero at Punta Sargento (Lat. $29^{\circ}18'$) including both sides of the Infiernillo, and a small population of *Avicennia* farther north at Puerto Lobos (Lat. $30^{\circ}16'$). In Baja California north to Bahía Las Animas (Lat. $28^{\circ}50'$), and small communities at the south end of Bahía de Los Angeles and nearby Isla Smith (Lat. $29^{\circ}05'$).

salt scrub

Salt grasses, halophytic shrubs (salt bushes), and succulent forbs. Salt-flats, beaches, and mangrove margins (Fig. 3). Salt grasses, e.g., *Jouvea pilosa*, *Monanthochloe littoralis*, *Sporobolus virginicus*. Halophytic shrubs (salt bushes), e.g., *Atriplex barclayana*, *Tricerma phyllanthoides*, *Suaeda torreyana*. Succulent herbs and shrubs, e.g., *Allenrolfea occidentalis*, *Batis maritima*, *Salicornia* spp.



FIGURE 2. White mangrove, *Laguncularia racemosa*, at low tide in Estero Sargento, Sonora. Note pneumatophore development of this solitary shrub.



FIGURE 3. Northeast side of Isla Alcatraz. Very sparse mixed desert scrub in foreground, with immature *Pachycereus pringlei* (*cardón*), *Lycium brevipes*, and *Viscainoa geniculata*; a single *Lemaireocereus thurberi* (organ-pipe) at lower right. *Amaranthus watsonii* nearly carpets the foreground. The low dense vegetation in background is salt scrub comprised largely of *Allenrolfea occidentalis*.

3. *Desertscrub*.—Covers most of the land surface of the northern Gulf region and is comprised of many distinctive communities. We classify the desertscrub of this region into six major community types, as follows:

coast scrub

Low monotonous coastal vegetation with few species, dominated by *Frankenia palmeri*. In Sonora from the head of the Gulf south to the vicinity of Punta Baja, and on Isla Tiburón.

creosotebush scrub

Simple communities dominated by *Larrea divaricata* (creosotebush). Widespread at the head of the Gulf, from near sea level to peak elevation on Sierra Pinacate. In the mid-Gulf, in the region of Isla Tiburón (Fig. 4) and the adjacent coast, occurring in limited zones at lower elevation, and to about 350 m on particularly dry slopes (e.g., Sierra Menor, Isla Tiburón). Near its southern limit in Sonora, in the vicinity of Guaymas, restricted to exposed low-elevation rolling hills

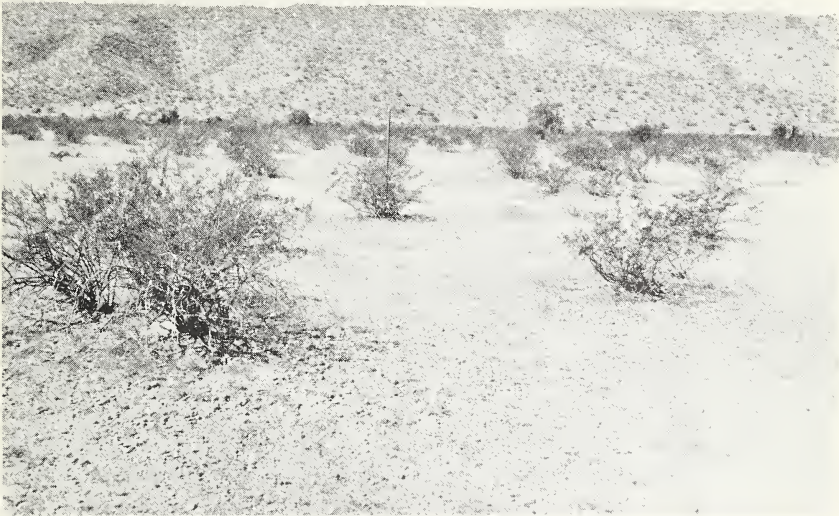


FIGURE 4. Creosotebush scrub (*Larrea divaricata*), Agua Dulce Valley, near center of Isla Tiburón. Lower slopes of Sierra Menor in background (looking west). The pole in center is 1.5 m tall.

and ridges; and at limited flatland sites south of Empalme, mostly on disturbed sites.

mixed desertscrub

The most widespread and characteristic terrestrial vegetation of the northern Gulf region (Figs. 3, 5, 6, 7). Highly varied in life-form of taxa, with numerous small-leaved and drought-deciduous shrubs and sub-shrubs. Seasonally rich development of ephemerals; each season with a different species spectrum although primarily differentiated into winter-spring and summer-fall sets. Dominance shared primarily by desert shrubs and small desert trees that comprise many distinctive, usually local community types. Representative species are:

Bursera microphylla
Cercidium microphyllum
Citharexylum flabellifolium
Colubrina viridis
Desmanthus fruticosus

Jatropha cuneata
Lippia palmeri
Pithecellobium confine
Ruellia californica
Viscainoa geniculata



FIGURE 5. Aerial view of the coastal bajada and dissected bluffs of the Infiernillo coast between Bahía Kino and Punta Chueca, Sonora, 1964. The relatively evenly spaced shrubs are mixed desertscrub. The watercourses here do not support distinct riparian vegetation.

cactus scrub

Dominance primarily or in part by columnar cacti, e.g., *Carnegiea gigantea*, *Lemaireocereus thurberi*, *Lophocereus schottii*, *Machaerocereus gummosus*, *Pachocereus pringlei*, *P. pecten-aboriginum*. Localized zones and regions primarily south of the vicinity of Puerto Lobos, Sonora, and on certain of the islands; particularly well-developed on Isla Cholludo (Fig. 8). Maximum regional development in coastal areas near the southern end of the desert. Often locally called *saguaral* (saguaro, *Carnegiea gigantea*) and *cardonal* (cardón, *Pachocereus pringlei*) (Fig. 9).

riparian desertscrub

Characterized by desert trees and shrubs peculiar to desert arroyos, washes, and their floodplains (Figs. 10, 11, 12). For example:

<i>Acacia greggii</i>	<i>Hyptis emoryi</i>
<i>Ambrosia ambrosioides</i>	<i>Olneya tesota</i>
<i>Bumelia occidentalis</i>	<i>Prosopis torreyana</i>
<i>Cercidium floridum</i>	<i>Stegnosperma glandulosa</i>
<i>Hymenoclea monogyra</i>	<i>Vallesia glabra</i> .

In addition, in desertscrub (e.g., creosotebush scrub), with less than about 125-150 mm (ca 5-6 inches) rainfall, many desert species



FIGURE 6. Arroyo Limantur, east side of Isla San Esteban. Sparse cactus scrub and mixed desertscrub elements, including *Pachycereus pringlei* (cardón), *Machaerocereus gummosus* (pitahaya agria), *Opuntia ciribe* (cholla), and *Atriplex barclayana*.

that are elsewhere non-riparian (e.g., *Cercidium microphyllum*) are often restricted to the dendritic (riparian) drainageways.

riparian aguajes, or tinajas

Desert fresh-water communities, usually highly localized at and near spring source "waterholes" that support the reed *Phragmites australis* and/or other spring supported species such as *Cyperus elegans*, *Eleocharis geniculata*, *Salix gooddingii*, and *Typha domingensis*.

Ecotones of Desertscrub and Thornscrub

In the area treated, particularly in its southern part, there are many ecotones between desertscrub and thornscrub. Some of the ecotones occur over relatively small areas that often involve local floodplains and arroyos. Others cover extensive areas of many hundred square kilometers. In fact, the entire arborescent subdivision of the Sonoran Desert, which Shreve (1951, p. 43) referred to as the Foothills of Sonora, is a broad inland Madrean foothill ecotone of thornscrub. It is situated between the Sonoran Desert proper and the more southerly Short-tree Forest (*sensu* Gentry 1942) of the coastal northwestern Mexican mainland (Felger 1976-2).



FIGURE 7. Mixed desertscrub and cactus scrub elements, ca 25 km inland from the vicinity of Puerto Libertad, Sonora. Prominent species here include *Cercidium microphyllum* (foothill palo verde), *Carnegiea gigantea* (saguaro), *Pachycereus pringlei* (cardón), *Lemaireocereus thurberi* (organ-pipe), *Lophocereus schottii* (senita), *Opuntia fulgida fulgida* (jumping cholla), and *Opuntia bigelovii* (teddybear cholla). Shallow arroyos or washes in center and background support poorly differentiated riparian desertscrub with *Cercidium microphyllum* and *Olneya tesota* (ironwood).

Within the Sonoran Desert proper, as restricted above, there are several areas of higher elevation with floristic and vegetative aspects of both thornscrub and desertscrub. Three of the principal ones are (1) north-facing slopes and higher elevations in the mountains northwest of Guaymas, between Bahía San Carlos and Ensenada Grande (=San Pedro Bay), Sonora, (2) Sierra Kunkaak on Isla Tiburón, and (3) intermediate elevations in the Sierra de la Giganta, Baja California Sur.

4. *Thornscrub*.—Complex dry-deciduous subtropical vegetation with dominance usually shared by many small trees and large shrubs. Seasonal aspects sharply distinctive, with wet-season perennial coverage on the order of 50-100 percent. The two major forms in the Gulf region are (1) plains thornscrub and (2) foothill thornscrub, with a larger component of tree species.



FIGURE 8. Isla Cholludo, showing about half of the northern portion of the island. Dense cactus scrub including *Pachycereus pringlei* (cardón), *Lemaireocereus thurberi* (organ-pipe), and *Opuntia fulgida* (jumping cholla).



FIGURE 9. Cactus scrub (cardonal) on sandy soil at Punta Baja, Sonora. The cacti are *Pachycereus pringlei* (cardón), *Lemaireocereus thurberi* (organ-pipe), *Lophocereus schottii* (senita), and *Opuntia fulgida* mammillata (jumping cholla).

plains thornscrub

Low spiny scrub varying in density from closed canopy to savanna-like vegetation. Savanna-like areas are largely not climax vegetation. Mixture of subtropical scrub and southern desert species, including facultative shrubs that here assume arborescent life-form. Lowlands of southwestern Sonora and coastal margins of extreme northwestern Sinaloa; synonymous with Thorn Forest (*sensu* Gentry 1942). Characteristic species include:

Acacia cochliacantha

Cercidium praecox

Forchammeria watsonii

Fouquieria macdougalii

Guaicacum coulteri

Jacquinia pungens

Lemaireocereus thurberi

Opuntia wilcoxii

Pachycereus pecten-aboriginum

Pithecellobium sonorae.

foothill thornscrub

Low shrubby or semi-arborescent scrub, often with nearly closed canopy of small trees and large shrubs. Along the southeastern margin



FIGURE 10. Northeast side of Isla Dátil (=Turners Island). Dense, brushy vegetation on north- and east-facing slopes at head of small canyon, with riparian desertscrub aspects. *Pachycereus pringlei* (cardón), *Fouquieria splendens* (ocotillo), *Lemaireocereus thurberi* (organ-pipe), and various shrubs including *Lycium brevipes*, *Colubrina viridis*, *Jatropha cuneata*, *Solanum hindsianum*, *Olneya tesota* (ironwood), and *Simmondsia chinensis* (jojoba).

of the Sonoran Desert it is largely synonymous with Shreve's (1951) Foothills of Sonora. Also locally in Baja California Sur and at higher elevations within the Sonoran Desert near its southern margins. For example:

Bursera fagaroides

Ceiba acuminata

Elytraria imbricata

Fouquieria macdougalii

Haematoxylon brasiletto

Jatropha cordata

Karwinskia humboldtiana

Ipomoea arborescens

Lysiloma divaricata

Pachycereus pecten-aboriginum.

riparian thornscrub

Thornscrub communities—and mixed thornscrub desertscrub communities—peculiar to certain types of arroyos, washes, and their floodplains. There are numerous characteristic species. For example:

Ambrosia ambrosioides

Coccoloba standleyi

Guazuma ulmifolia

Lysiloma candida



FIGURE 11. Agua Dulce Valley, near center of Isla Tiburón. Riparian desertscrub. The tree is *Bumelia occidentalis*, and the shrubs are *Olneya tesota* (ironwood) and *Hyptis emoryi* (desert lavender).



FIGURE 12. Riparian desert scrub at Ensenada Grande (=San Pedro Bay), Sonora. *Lysiloma candida* (palo blanco) with dense understory of small shrubs including *Randia*, *Ruellia*, and *Croton*. This is the only known locality for *Lysiloma candida* outside of Baja California.

*Ficus petiolaris**Lysiloma divaricata**Ficus paduifolia**Perisklopsis porteri**Gouania rosei**Vallesia baileyana*.

5. *Short-tree Forest*.—Semi-arid subtropical dry-deciduous forest of small trees (Gentry 1942). Not in the northern part of the Gulf of California. Occurrence in the coastal border Gulf vegetation in southern and central Sinaloa. Also at intermediate elevations in southeastern Sonora, and the Cape Region of Baja California Sur.

SHORELINE VEGETATION

Shoreline vegetation in the Gulf of California occurs in several distinctive physical habitats that support highly distinctive plant communities. Three of the more distinct ecological situations—shoreline habitats—are (1) the *sea cliff*, (2) the *beach dune*, and (3) the *salt flat*. Lying between these edaphic extremes and the unique plant communities that they support, are the average sandy-gravelly-rocky desert substrata which stretch across the extensive coastal plains, hills and mountains and support desertscrub communities in a complex pattern of continua and mosaics.

Sea Cliff Vegetation.—On vertical rocky sea cliffs relatively free of bird guano (sea cliffs with bird rookeries often accumulate extensive deposits of guano), a unique group of rock-holding plant species comprise a very sparse vegetation. Prominent in these communities are *Ficus petiolaris palmeri*, *Hofmeisteria crassifolia*, *H. fasciculata*, *Eucnide rupestris*, *Pleurocornis laphamioides*, and in the vicinity of Bahía San Pedro, even the palm *Erythea clara*. The rock-face sea cliff community is a natural extension from that of the tropical and subtropical canyon rock cliff habitat. Thus a few of the hardiest canyon cliff species also persist on arid and semi-arid tropical and subtropical sea cliffs. The plant components of the sea-cliff vegetation in the Gulf of California region are highly predictable. They provide an especially clear-cut example of the fact that the natural community owes its existence to the simple overlap of the spans of the genetically controlled ecological tolerances of the comprised species.

Beach Dune Vegetation.—Coastal dunes occur along much of the Gulf Coast of Sonora and on Isla Tiburón, and on parts of the Gulf Coast of Baja California. High unstable dunes facing the sea are commonly built along extensive stretches of shore. Proceeding inland there may be progressively smaller and more stable dunes positioned in parallel series. The more inland ones are of older age than the present outer beach dune. Although there is a gradual geographic replacement or shift in the dune flora from north to south—and, to a lesser extent, on the climatically different east and west sides of Isla Tiburón—in any one Gulf Coast area (e.g., the Tastiota area, and Puerto Libertad area, etc.) the dune flora is highly predictable from dune to dune, depending on (1) dune size, (2) dune stability, and (3) exposure to maritime wind.

Many dune species have deep roots, and there is a preponderance of silvery or grey-pubescent leaved plants in the community. Certain characteristic dune species seldom occur elsewhere, e.g., *Astragalus magdalenae*, *Dicoria canescens*,

Euphorbia leucophylla, and *Triteliopsis palmeri*. Others on the dunes are characteristically sandy-soil species with wide distribution in sandy non-dune habitats, e.g., *Abronia maritima*, *A. villosa*, *Aristida californica*, *Croton californicus*, *Dalea emoryi*, *Helianthus niveus*, and *Jouvea pilosa*. Still other common species on dune sand occur over a conspicuously wider spectrum of substrata, e.g., *Atriplex canescens*, *Lycium brevipes*, *Palafoxia arida*, *Prosopis glandulosa torreyana*, and *Sesuvium verrucosum*. A few species, such as *Jouvea pilosa*, are confined exclusively to the sea-facing coastal dune slopes, and do not occur on the lee slopes. Ephemerals may be seasonally abundant and well developed, especially in the more stable areas of the coastal dunes.

Salt-flat Vegetation.—Where flat land slopes nearly imperceptibly toward the sea, salt flats occur with their characteristic halophytic vegetation. Very slight elevational differences, often on the order of much less than one meter, are capable of producing marked as well as abrupt vegetational and floristic transitions to desert-scrub adjacent to and within salt flat areas. Hence, these adjacent and divergent communities characteristically form a conspicuous mosaic pattern obviously under edaphic control.

Significant to the halophytic community composition are the length of time between floodings and the distance from the sea. Salt-flats behind beaches and coastal dunes may be subject to flooding only at the highest tides of the year or during summer rains, e.g., the Llanuras de San Juan Bautista. Elsewhere daily tides may inundate the soils near bays (e.g., in the vicinity of Bahía de la Cholla and Puerto Peñasco), and areas adjacent to mangrove inlets or esteros. Representative salt-flat species include *Allenrolfea occidentalis*, *Atriplex linearis*, *Batis maritima*, *Frankenia grandiflora*, *Monanthochloe littoralis*, *Tricerma phyllanthoides*, and *Suaeda torreyana*. Ephemerals are few and poorly developed or absent.

THE ISLANDS

There is no permanent settlement on the eight islands treated here, and the ecosystems of these islands remain in an essentially natural state. Checklists for the vascular plants known to us for each of the eight islands are given in Table 1, a statistical summary of the flora is presented in Table 2 (see pp. 54-56), and pertinent geographical information is given in Table 3 (see p. 57). Island areas given here are based on the most recent, available maps (also see Soulé and Sloan 1966, and Tamayo 1949).

THE SERI INDIANS AND ISLAND FRESH WATER

Since ancient times the Seri Indians occupied both Isla Tiburón and Isla San Esteban as well as the opposite Sonora coast (Bowen, in press; Moser 1963; Felger and Moser 1975-b, 1976). These people, traditionally a hunting and gathering and seafaring society, practiced no agriculture in this region. During traditional times their impact on the vegetation and fauna, from which they derived their subsistence, was probably minimal (see Felger and Moser 1970, etc.; Felger 1976-b). Permanent

watering places, all with limited supply of fresh water, are well distributed on Tiburón. Fresh water on Isla San Esteban was extremely limited, and sometimes gave out during periods of drought that forced the resident Seri to move temporarily across the channel to Isla Tiburón (Moser 1963). There is now, and was previously no permanent fresh water on any of the other Sonoran islands and, consequently, they were not occupied by native people. Brief bird guano mining operations were carried out with transported water on Isla San Pedro Mártir and on Isla Patos earlier in this century.

ISLA TIBURÓN

With an area of about 1210 km², Isla Tiburón is the largest island on the Pacific Coast of North America south of Canada. Its geology, topography, climate, and vegetation are complex. Peak elevation is 875 m. Gentry (1949, p. 94) provides the following sketch of the island:

It is separated from the Sonoran mainland by a shallow narrow channel, "el infiernillo," two to five kilometers wide and only three to four meters deep. Roughly quadrangular in shape, the island contains about 1170 square kilometers. Although mountainous, there are extensive valleys. . . . There are two igneous ranges of mountains trending north and south and paralleling the adjacent ranges of Sonora. The western is Sierra Menor, the eastern and higher is Sierra Kunkaak . . . the shallow infiernillo channel was emerged repeatedly during the low sea levels of the glacial periods.

Through warfare and pestilence, Seri population greatly dwindled towards the latter part of the last century, and their numbers became even more drastically reduced in the first half of this century. During this time Tiburón remained their refuge and undisputed homeland, if for no other reason than because this insular desert provided an effective retreat from the military (see Spicer 1962). From about 1955 until the present time the island has been little occupied. Wildlife management and limited military installations and roads were established in 1967. During 1975 the president of Mexico decreed that the island be given to the Seri tribe.

The vegetation of Isla Tiburón includes extensive areas of littoral scrub, desert-scrub, and thornscrub, as well as coastal seagrass meadows. Each major community-type occurring in the northern Gulf Coast of Sonora is found on the island.

The vegetation of Sierra Kunkaak (elevation 875 m) includes substantial areas of thornscrub and thornscrub-desertscrub ecotones. The higher elevations and portions of the east- and north-exposure slopes support extensive stands of nearly closed-canopy *Lysiloma divaricata* (*mauto*). Their maximum height is considerably less than in the mainland short-tree forest (*sensu* Gentry 1942) of southeastern Sonora. Riparian thornscrub extends along major canyons into the lower elevations at the base of Sierra Kunkaak.

Most of the area of the island is covered with desertscrub of diverse structure and composition. Coast desertscrub communities dominated by *Frankenia palmeri* occur along all shores of the island that are of gentle topography. The most extensive development of coast desertscrub is along the east shore where the expansive island bajada gradually dips toward the sea.

Extensive areas dominated by *Larrea divaricata* (creosotebush) occur on the plains of the Agua Dulce Valley towards the interior of the island (Fig. 4). These simple communities are located between shallow drainageways supporting small desert trees and shrubs. This mosaic involving creosotebush scrub, mixed desert-scrub, and riparian desertscrub is in a dendritic-reticulate pattern with the overall drainage coursing northward through the Agua Dulce Valley and issuing into the sea near Tecamate at the northeast end of the island. Another conspicuous area of creosotebush scrub occurs along the east side of the island. Here *Larrea* shares dominance with *Cordia parvifolia* in a narrow zone parallel to the Infiernillo shore and situated between coast desertscrub and the more inland, and complex mixed desertscrub communities.

Mixed desertscrub, with dominance shared by numerous desert shrubs, covers the majority of the lowlands and western mountains (Sierra Menor) of the island. The mixed desertscrub communities reach maximum species richness and highest density on the gentle upper reaches of the extensive bajada slope facing the Canal del Infiernillo, on the east side of the island. Distribution of major perennials across this bajada is surprisingly even, and more or less mirrors the pattern of that on the opposite mainland coast (see Fig. 5). On the more harsh and exposed portions of Sierra Kunkaak, such as southward- and westward-facing slopes, mixed desertscrub communities extend to peak elevation.

Cactus scrub with conspicuous "forests" of columnar cacti occur primarily along the east side of the Agua Dulce Valley which drains into Bahía Agua Dulce (vicinity of Tecamate). Here the valley floor slopes gradually westward and supports a relatively large population of *Carnegiea gigantea* (saguaro), small desert trees (e.g., *Cercidium microphyllum*), and an array of desert shrubs. Slope exposure compares well with that of the bajada of the mainland side of the Infiernillo where extensive stands of the more maritime *Pachycereus pringlei* (*cardón*) occur, rather than saguaro. Saguaros near the Gulf characteristically attain maximum development on more island sites, while *cardón* is relatively more abundant in immediate coastal situations. The fewer dense stands of *cardón*-dominated cactus "forest" (*cardonal*) on Tiburón may be due, in part, to the absence of extensive west-facing and south-facing coastal bajadas; it may be due also to subtle controls of topography and microclimate, including the east to west decreasing precipitation gradient on and near the island. Relatively dense but localized stands of *cardón* occur here and there on lower slopes within mixed desertscrub, such as in the vicinity of the Sauzal water-hole, and elsewhere as on the east side bajada facing the Infiernillo.

Riparian desertscrub is especially well developed along the extensive dendritic arroyo systems draining the island. The extensive Arroyo Agua Dulce system that drains the interior valley supports many miles of riparian desertscrub. Especially noteworthy are plant species in the upper reaches of the interior valley with individuals of enormous size relative to their usual maximum size elsewhere in the Sonoran Desert, e.g., *Bumelia occidentalis* at 11 m (36 feet) height (Fig. 11), *Condalia globosa* at 5.5 m (18 feet), and *Koeberlinia spinosa* at 5.5 m.

Isla Tiburón is the only Sonoran island with riparian *aguajes* or *tinajas*. One of the more permanent watering places is Sauzal, near the south-central end of the island. Most of the others occur scattered through Sierra Kunkaak.

Well developed littoral scrub occurs along the shores of the island, and reaches maximum development on the east shore bordering the protected Infiernillo coast, which has a number of lagoons and expansive beaches. There are three major esteros, all with extensive mangrove scrub, on the Infiernillo shore: Punta Perla at the north, Palo Fierro at about midway, and Santa Rosa at the south end of the Infiernillo. The three species of mangrove are present. Salt scrub occurs along the shores nearly throughout the island. It is absent only where sea cliffs and steep rock slopes reach directly down into the sea, such as along portions of the southern and western shores. Extensive seagrass meadows occur in the Canal del Infiernillo, and *Zostera marina* and *Ruppia maritima* are seasonally abundant in the beach drift on the east side of the island.

The central relief and area of Isla Tiburón are extensive enough to produce several distinctive climatic zones and hence distinctive phytogeographic areas. Two are especially noteworthy: (1) thornscrub and thornscrub-desertscrub ecotone at higher elevations on Sierra Kunkaak and (2) the relatively xeromorphic desertscrub on the drier western margin of the island.

Sierra Kunkaak.—The subtropical thornscrub of Sierra Kunkaak is comprised largely of species and communities that are often northern outliers disjunctive from subtropical regions much farther southward. Some of these populations are separated from their nearest conspecific populations by much or all of the intervening areas of the Sonoran Desert. Their insular distribution on Tiburón is like an island within an island. Examples are *Ayenia glabra*, *Croton magdalenae*, *Guaiaacum coulteri*, and *Lasiacis sorghoides*.

The Western Margin.—The vegetation on Tiburón reveals a strong east-west climatic gradient, but only a slight one from north to south. The vegetation on the western Gulf side of the island lying in the summer rain-shadow of Sierra Kunkaak, is conspicuously more xeromorphic than that of the eastern (Sonora) side bordering the Infiernillo. The far western arid margin of Tiburón, largely on the western side of the crest of Sierra Menor, supports certain species which otherwise occur primarily on the Baja California side and/or at the arid head of the Gulf. Examples are *Ambrosia ilicifolia*, *Cassia confinis*, *Drymaria holosteoides*, and *Pelucha trifida*.

Baja California species occurring on Tiburón, and in some cases also on other Gulf islands, but not on the opposite mainland of Sonora include 4.2 percent of the flora. These are:

Acalypha comoduana
Antirrhinum kingii
Cassia confinis
Castela polyandra
Cryptantha angelica
Dalea vetula
Drymaria holosteoides
Euphorbia magdalenae
Fagonia palmeri
Passiflora palmeri
Pelucha trifida
Porophyllum crassifolium.

For the most part, however, the lowland regions of Tiburón support a flora which is almost identical with that of the Sonoran mainland directly opposite the island. Three Old World species, now widely naturalized in the New World, have become well established in the interior of the island: *Chenopodium murale*, *Mollugo cervinana*, and *Tamarix ramosissima*.

We have located 286 species on Tiburón (Table 1). An additional 10 to 15 percent may reasonably be expected to occur, and most of the new additions will come from the higher elevations of Sierra Kunkaak. The flora of this largest island in the Gulf of California contains no known endemic plant species. All of the species present also occur either on the mainland of Sonora and/or the peninsula of Baja California.

ISLA SAN ESTEBAN

Isla San Esteban lies in mid-Gulf 11.6 km south from the southwest shore of Isla Tiburón. Its more or less compact rectangular shape covers about 43 km². High sea cliffs edging the island are interrupted by widely-spaced canyons, and on the east side by a broad valley-like canyon known as Arroyo Limantur (Fig. 6). A rugged horseshoe-shaped series of mountains, rising to 550 m elevation, surround Arroyo Limantur.

The small band of Seri Indians inhabiting San Esteban were exterminated by the military in one tragic event during the 1860's (Moser 1963). The island has since been uninhabited and remains in a primordial state, scarcely altered by man.

Mixed desertscrub with a preponderance of cactus scrub elements dominates the landscape. The communities are xeromorphic, some extremely so, and surprisingly diverse and varied. Communities along the major arroyos, including Arroyo Limantur, are scarcely differentiated as distinctive riparian desertscrub. Some elevational zonation is apparent, although generally weaker than community differences along slope-exposure gradients (e.g., north-south). Very limited salt scrub communities, occupying restricted areas behind some of the high cobble beaches, consist primarily of *Suaeda torreyana* and *Atriplex barclayana*.

Among the most prominent elements of the desertscrub vegetation on San Esteban are:

- Agave dentiens*
- Atriplex polycarpa*
- Bursera microphylla*
- Colubrina viridis*
- Echinocereus grandis*
- Jatropha cuneata*
- Machaerocereus gummosus*
- Mammillaria estebanensis*
- Olneya tesota*
- Opuntia ciribe*
- Pachycereus pringlei*
- Simmondsia chinensis*
- Solanum hindsianum*.

We have collected 107 species on San Esteban (Table 1) and the flora may contain an additional 10 percent. Two cacti, *Echinocereus grandis* and *Mammillaria estebanensis*, are endemic to the Islas San Lorenzo and San Esteban. *Agave dentiens*, closely allied to *A. deserti* and probably not distinct at the specific level, occurs on several other islands on the Baja California side of the Gulf. *Lyrocarpa linearifolia* is otherwise known only from Isla Angel de la Guarda.

Most of the flora is common to both sides of the Gulf. However, the general physiognomy of the vegetation and phytogeography of a portion of the flora shows close affinity with the desertscrub of Baja California. Plants known otherwise only from Baja California and other Gulf islands represent 11.3 percent of the island's flora. These are:

Agave dentiens
Argemone subintegrifolia
Chloris brandegeei
Echinocereus grandis
Haplopappus spinulosus incisifolius
Lycium megacarpum
Lyrocarpa linearifolia
Mammillaria estebanensis
Opuntia ciribe
Passiflora palmeri
Porophyllum crassifolium
Sideroxylon leucophyllum.

ISLA SAN PEDRO NOLASCO

This rugged and precipitous island lies in deep water and geologically has long been isolated from the mainland. On either side of a prominent north-south ridgecrest running the length of the island, the terrain quickly falls away into the sea with many short, steep and highly eroded canyons. Maximum elevation is 318 m. High sea cliffs, edging the entire island, harbor extensive sea bird rookeries and are white with guano. The island area is approximately 3.5 km². There is no fresh water on the island and it has never been inhabited by man. Its terrestrial ecosystem is virgin.

The vegetation is comprised of desertscrub that is sharply divided into unique communities segregated according to slope exposure. The communities show a relatively discontinuous or mosaic pattern of distribution that is exceptionally clear where the environmental gradients on the slope exposures change abruptly. Otherwise a continuum pattern is evident.

The northerly oriented slopes on the east side of the island, exposed to strong sea moisture-laden breezes, support meadows of grasses and forbs. Ground coverage is generally at or near 100 percent. Comparable communities do not exist elsewhere in the Gulf Coast region of Sonora. Soil profiles are deep and rich in organic material. Soil erosion is at minimum, despite the steepness of these north-facing slopes. Yet the steepness of slope is noticeably less than on adjacent south-facing slopes, undoubtedly due to the lower rate of erosion. Some prominent north-facing

species are: *Amaranthus fimbriatus*, *Bothriochloa barbinodis*, *Coreocarpus arizonicus*, *Muhlenbergia microsperma*, *Perityle californica*, *Setaria macrostachya*, *Trichachne californica*, *Trichloris crinata*, and *Vaseyanthus insularis*.

East-facing slopes consist primarily of broad ridges separating north-facing and south-facing canyon slopes on the east side of the island. *Agave chrysoglossa*, *Opuntia wilcoxii*, *Salvia similis* and others are, with minor exception, restricted to these slopes. The smaller cacti (*Echinocereus* and *Mammillaria*) and various other species reach maximum development and density on east-facing slopes. Other prominent east slope species include *Acacia willardiana*, *Lemaireocereus thurberi*, *Pachycereus pringlei*, *Colubrina viridis*, and *Viguiera deltoidea*.

The general physiognomy and vegetation on south-facing slopes on the east side of the island and most of the west side of the island are closely akin. Large expanses of bedrock are exposed at the surface. Conspicuous plants are columnar cacti (*Lemaireocereus thurberi* and *Pachycereus pringlei*), simple-leaved and xerophytic desert shrubs (e.g., *Jatropha cuneata* and *Viguiera deltoidea*), and small cacti (*Echinocereus websterianus* and *Mammillaria multidigitata*). Ephemerals and grasses are usually poorly developed. The flora shows close affinity with the adjacent Sonoran coast.

We have found 55 species of plants on the island (Table 1). This is the only Sonoran island with single-island endemics. These are three species of cacti which seem to be derived from mainland Sonoran taxa: *Echinocereus websterianus* from *E. pectinatus* var. *scopularum* (Lindsay 1947), *Mammillaria multidigitata* possibly from *M. thornberi* (= *M. fasciculata*), and *M. tayloriorum* from the *M. sonorensis* complex (Glass and Foster 1975). Several extra-limital populations are noteworthy. *Salvia similis* is otherwise known only from Baja California, and *Euphorbia magdalenae* from Baja California and Isla Tiburón. *Metastelma pringlei* has previously not been reported from Sonora, and is primarily known from the Sierra Madre Occidental. [It may also occur in Baja California (Wiggins 1964, p. 1122)]. *Mollugo verticillata* is the only non-native species and has become well-established on the island.

ISLA SAN PEDRO MÁRTIR

Isla San Pedro Mártir, lying in deep water in the mid-Gulf, is the most isolated island in the Gulf of California. Apparently of volcanic origin, it is doubtful if it ever has been connected to any other landmass. There are no beaches, alluvial deposits, or outwashes. Most of the surface of the island is exposed and offers little or no shelter from wind. Maximum elevation is 320 m and most of the surface comprises high plateaus lying above 150 to 200 m. The island area is about 1.5 km². Sea cliffs are the principal coastal features and support enormous numbers of sea birds and thick guano deposits. During the cooler months of the year the upper elevations are often shrouded in fog which seems to provide the vegetation with significant moisture. The climate appears to be extremely arid.

There is no fresh water on the island. It was inhabited temporarily by guano miners, prior to World War II, whose activities centered around the guano-covered

periphery. On the whole, the island vegetation today appears to be natural and undisturbed.

The sparse desertscrub consists of cactus scrub and mixed desertscrub elements. Elevational zonation is apparent, with gradually increasing species richness and vegetation density towards higher elevation. At lower elevation, on the guano-covered sea cliff edges of the island, there is essentially no vegetation.

Among the most conspicuous and abundant perennials are *Pachycereus pringlei* (cardón) and *Sphaeralcea hainesii*. Ephemerals seasonally produce extensive ground cover, e.g., *Aristida adscensionis*, *Euphorbia petrina*, *Mentzelia adhaerans*, *Perityle californica*, and *Vaseyanthus insularis*.

The flora is relatively depauperate and the species known to us total 23 (Table 1). Further exploration will probably not yield more than a few additional species. Relatively extreme aridity and little habitat diversity are principal factors contributing to the depauperate flora for an island this large in the island series. Isolation by distance is undoubtedly another contributing factor. There are no endemic plants and most of the flora is common to both sides of the Gulf. Species occurring otherwise only on other Gulf islands and Baja California are *Sphaeralcea hainesii* and *Pelucha trifida*.

ISLA DÁTIL

Isla Dátil (=Turner's Island) is a narrow, north-south oriented, former mountain lying at the southern end of a partially submerged peninsula extending southward from the southeast shore of Isla Tiburón. Reefs connect Islas Dátil and Cholludo and both appear to be rather recent fragmentations from Tiburón (Lowe 1955).

The rugged topography offers a wide range of microenvironments. Peak elevation is 183 m, and the total area about 1.5 km². There are a few small rock beaches but most of the shore consists of high sea cliffs. There are several major canyons.

The vegetation consists almost wholly of mixed desertscrub and some riparian desertscrub. Salt scrub species, e.g., *Suaeda torreyana*, are present behind the few small cobble beaches, but do not form distinctive communities.

Vegetation on Isla Dátil is noticeably more dense and "brushy" than on the adjacent south shore of Isla Tiburón, and is likewise distinctive from other Gulf islands. East-facing and north-facing canyon slopes and canyon floors support dense desertscrub that may be termed riparian (Fig. 10). However, the distinction on this island between riparian and non-riparian vegetation is not sharp. The communities with maximum species richness occur on north-facing slopes near the summit on the east side of the island. Most of the island, however, supports relatively xeromorphic desertscrub, and south-facing slopes are sparsely vegetated.

The flora is surprisingly rich (99 species, Table 1) for this relatively small island satellite of Tiburón. An undescribed *Mammillaria* is endemic to both Isla Dátil and Isla Cholludo. It shows affinity with *M. dioeca* of Baja California and California (Robert Foster, *personal communication*), and appears to be distinct at the subspecific level. Otherwise there is no indication of endemism on the island. For the most part, the flora shows affinity with the nearby south side of Isla Tiburón;

although there are some notable extra-limital populations on Isla Dátil. *Calliandra californica* is an outlier from Baja California, while *Coldenia canescens*, a xerophytic species of the northern part of the Sonoran Desert, is widely disjunct southward onto Isla Dátil. The exceedingly rich flora seems to result from the locally favorable maritime climatic conditions, the highly varied island topography providing a relatively wide range of microenvironments, and the relative proximity of the island to major land masses including Isla Tiburón. Furthermore, larger herbivores, such as mule deer and rabbits, are absent on this island although present on Tiburón.

ISLA ALCATRAZ

Isla Alcatraz (or Isla Pelicano, or Isla Tassne) lies 1.4 km offshore in Bahía Kino, with a channel not more than two fathoms deep. Its isolation from the mainland presumably has been of short duration.

The island has two distinctive topographic parts, each comprising roughly one-half of the island area. The northeastern part is relatively flat and not more than one to two meters above mean high tide level. The southwestern portion rises steeply into a rocky mountain mass of approximately 130 m elevation. The island area is about 0.5 km². Vegetation, flora, and white bird guano deposits from extensive sea bird rookeries are sharply distributed according to these major topographic features. There is no fresh water on the island, and although it has been frequently visited, it is not known to have been occupied by man.

The extensive low flat on the northeast side of the island supports salt scrub and meager isolates of desertscrub (Fig. 3). Much of the interior portion of this flat consists of a low-lying playa dominated by *Allenrolfea occidentalis*. Sparse stands of herbaceous salt scrub species are strewn along the upper beach. The low statured and very open mixed desertscrub occurs on low sandy rises between the small inland playa and the beaches.

The eastern slopes of the mountainous region supports a sparse cover of mixed desertscrub (Fig. 3). Differences in slope exposure, steepness, and drainage patterns produce moderately diverse but simplified communities of localized populations. Common species here are: *Amaranthus watsonii*, *Beloperone californica*, *Opuntia fulgida*, *O. phaeacantha*, *Nicotiana trigonophylla*, *Pachycereus pringlei*, and *Viscainoa geniculata*. Following periods of exceptional rains *Amaranthus watsonii* seasonally forms extensive and dense stands, which gives the island an appearance of being covered with grass as seen from the sea or the shore of Bahía Kino.

Aridity and extensive bird guano deposits render the southwestern and western portion of the island (or virtually all of the mountainous portion except its northeastern slopes) inhospitable to the development of vegetation. Principal plants found on this birdland are a few widely scattered *Pachycereus pringlei* and seasonally localized and relatively sparse stands of *Amaranthus watsonii*.

Proximity to the mainland and a moderate degree of habitat diversity allow a comparatively large number of species to exist over the eastern ⅓ of the island. The flora, moderately rich with 43 species (Table 1), shows obvious and close affinity

with the nearby mainland flora. Species of *Amaranthaceae*, *Cactaceae*, and *Chenopodiaceae* comprise the most widespread and dominant elements. Ephemerals (primarily *Amaranthus watsonii*) seasonally produce the major portion of the plant coverage of the desertscrub areas.

Opuntia phaeacantha is known from no other island, and the nearest population of this prickly-pear occurs near Punta Sargento. Several species are rare and probably not reproducing on the island, e.g., *Bursera microphylla*, *Encelia farinosa*, *Lophocereus schottii*, *Phaulothamnus spinescens*, *Prosopis glandulosa torreyana*, and *Tricerma phyllanthoides*. These appear to be recent arrivals.

ISLA PATOS

This small bird guano covered island lies in open water 7.3 km north of Isla Tiburón. A single conical peak rises 69 m above sea level. Total surface area is on the order of 0.4 km².

In 1946 the major perennials, mostly cacti, were deliberately destroyed and the island cleared to facilitate guano mining (see Gentry 1949). The commercial guano mining venture was short-lived. The island has otherwise remained uninhabited by man. There is no fresh water.

The highly xeromorphic desertscrub is very sparse and consists primarily of one chenopod (*Atriplex barclayana*) and two cacti (*Pachycereus pringlei* and *Opuntia fulgida*). Other species present form small populations that comprise an insignificant role in the vegetation.

The flora of Patos is the most depauperate of the eight Sonoran islands considered here, and we know of ten species to have been present:

Amaranthus fimbriatus (Torr.) Benth.

Atriplex barclayana (Benth.) Dietr.

Bouteloua barbata Lag.

Carnegiea gigantea (Engelm.) Britt. & Rose

Encelia farinosa A. Gray var. *phenicodonta* (S. F. Blake) I. M. Johnst.

Lophocereus schottii (Engelm.) Britt. & Rose var. *schottii*

Machaerocereus gunmosus (Engelm.) Britt. & Rose

Opuntia fulgida Engelm. var. *fulgida*

O. fulgida var. *mammillata* (Schott ex Engelm.) Coult.

Pachycereus pringlei (S. Wats.) Britt. & Rose

Trixis californica Kell.

We have found six vascular plant species on the island. *Carnegiea*, *Encelia*, *Machaerocereus*, and *Trixis* are now gone from Patos and apparently were not common even before 1946.

Additional exploration on the island will not yield at this time more than one or two additional species, and such, if present, will be ephemerals. A flora of ten species comprised of five cacti, three xeromorphic subshrubs, and two ephemerals indicates extreme aridity. Other major controlling factors may be small island target size and low relief.

ISLA CHOLLUDO

This tiny rock isle of roughly 0.1 km² is situated between Islas Tiburón and Dátil along a sunken peninsula that interconnects the three islands. Tamayo (1949) gives it the name Isla Lobos and some older American maps and papers use the name Isla Roca Foca or Seal Island. Cholludo is the name locally used. The south surface falls away abruptly to high sea cliffs. From the south ridge-crest, 75 to 100 m high, the surface of the island quickly slopes to the sea at the north shore. There are no arroyos and the isle is without a beach and without littoral scrub. The steep and rocky surface, with its northerly orientation, contains most of the surface area of the island and its vegetation. Isla Cholludo has never been occupied by man and is without fresh water. The biota remains in a virgin state.

The island is aptly named, for it is covered with a scarcely penetrable forest of cactus scrub, unique from its neighboring islands (Fig. 8). Dominant elements in this succulent landscape are *Pachycereus pringlei*, *Lemaireocereus thurberi*, *Opuntia fulgida*, and *Agave subsimplex*. *Perityle emoryi* seasonally produces a carpet of green among the spiny perennial cover.

The flora of this cactus garden isle is surprisingly rich. We have obtained 28 species (Table 1) on this small surface area, smallest of the eight islands in the series. Most of the species on Cholludo occur on neighboring Isla Tiburón and Isla Dátil. However, *Mammillaria dioeca*, common on Cholludo and Dátil, is unknown from Tiburón, and *Carnegiea* and several other species present on Cholludo have not been found on Dátil.

ISLA SAN JORGE

This vegetationless rocky guano-covered bird rookery is the northernmost of the islands discussed in this work. It is also known as Saint George Island or Georges Island. Johnston (1924, p. 1017) reported *Chenopodium murale* as "... the only phanerogam found on Georges Island ... The plant was no doubt introduced ... by guano workers and forms a few small colonies on talus loosened by blasting." Thus the only land plant ever recorded from the island is a species supposedly native to Europe and now extensively naturalized in North America. Our recent inspection of the island failed to reveal the presence of land plants.

FLORISTIC RELATIONSHIPS AND BIOGEOGRAPHY OF THE ISLANDS

Some accidental introduction of seeds from the mainland and from island to island by the continuing agency of man is likely, but intentional introduction by the Seri Indians is extremely doubtful (Felger and Moser, unpublished data). Only 4 species, or 1.2 percent of the flora of the Sonoran Islands, are non-native: *Chenopodium murale*, *Mollugo cerviana*, *M. verticillata*, and *Tamarix ramosissima*. These are indigenous to the Old World and are now widely naturalized in the New World. Their diseminules, in this case the seeds, are less than 1.5 mm in diameter. *Chenopodium murale*, an important traditional food of the Seri, was commonly

stored in pottery vessels (Felger and Moser 1976) and could have been accidentally introduced to new localities by the Indians. The small non-native component of the flora is undoubtedly related to the undisturbed, natural state of the islands' ecosystems. By way of comparison, the floras of San Clemente and Santa Catalina Islands, off Southern California, respectively contain 22.4 percent (69 species) and 29.7 percent (167 species) introduced species (Thorne 1969). The California islands have been extensively altered by man, livestock and other introduced exotics with devastating effects on the native ecosystems.

Most of the flora of the Sonoran islands is common to both sides of the Gulf of California. However, 7.6 percent of the flora of these islands is known otherwise only from Baja California and other Gulf islands. These are:

Acalypha comondwana
Agave dentiens
Antirrhinum kingii
Argemone subintegrifolia
Calliandra californica
Cassia confinis
Chloris brandegeei
Cryptantha angelica
Dalea vetula
Drymaria holosteoides
Echinocereus grandis
Euphorbia magdalenae
Fagonia palmeri
Haplopappus spinulosus incisifolius
Lycium megacarpum
Lyrocarpa linearifolia
Mammillaria estebanensis
M. dioeca
Opuntia ciribe
Passiflora palmeri
Pelucha trifida
Porophyllum crassifolium
Salvia similis
Sideroxylon leucophyllum
Sphaeralcea hainesii.

We expect additional botanical exploration will reveal that some of the Baja-insular "endemics" also occur on the Sonoran mainland. In contrast, we know of no plants from islands on the Baja California side of the Gulf which occur on the mainland of Sonora but not on Baja California—with the possible exception of *Opuntia fulgida*. On certain Gulf islands, such as Isla Angel de la Guarda, *Opuntia cholla* and *O. fulgida* are often confused; their biosystematic relationship is not clear.

Endemism on the eight Sonoran islands is low but not unusual for islands as close to shore as these and with small floras. It has long been known that endemism is much greater among the terrestrial vertebrates than for the flora on the Gulf islands

(Johnston 1924; Gentry 1949; Soulé and Sloan 1966). There are 8 taxa on the Sonoran islands which are endemic to one or more islands in the Gulf of California, representing 2.1 percent of the flora. These endemics are small cacti, one century plant, and one crucifer:

- Agave dentiens*, San Esteban and several other islands (?)
- Lyrocarpa linearifolia*, San Esteban and Angel de la Guarda
- Echinocereus grandis*, San Esteban and San Lorenzo
- E. websterianus*, San Pedro Nolasco
- Mammillaria dioeca* ssp. ?, Cholludo and Dátil
- M. estebanensis*, San Esteban and San Lorenzo
- M. multigitata*, San Pedro Nolasco
- M. tayloriorum*, San Pedro Nolasco.

Throughout their extensive ranges in North America, *Agave*, *Mammillaria*, and other small cacti such as *Echinocereus*, show extensive speciation with numerous taxa of limited geographic distribution. Although we list *Agave dentiens* as an endemic, its systematic status is in need of clarification.

San Pedro Nolasco, the only Sonoran island with single-island endemics, contains 3 endemics, representing 5.5 percent of the flora. The 4 island endemics on San Esteban, 3.7 percent of the flora, are shared with Islas San Lorenzo and Angel de la Guarda. While the number of endemics for all eight islands is low, the percentage of endemism for San Pedro Nolasco is comparable to that of certain islands off southern California. For example, San Clemente, lying 79 km offshore, has 13 endemics (5.4 percent of the flora), and Santa Catalina, 34 km offshore, has 7 endemics (1.8 percent) (Raven 1967; Thorne 1969).

As indicated by its specific name, *Lycrocarpa linearifolia* has leaves with reduced surface area relative to its congeners, an adaptation to the arid environment. Absence of large mammalian herbivores and different pollination ecology are probably among the strongest biotic selection factors acting on the remaining seven endemics. All of these are long-lived succulents and are animal-pollinated. *Echinocereus grandis* and *Mammillaria estebanensis* have unusually thick stems, or low surface-volume ratios—an adaptation well-suited for this extremely arid environment (see Felger and Lowe 1967).

There are no endemics on Islas San Pedro Mártir, Alcatraz, or Patos. None are known from Tiburón. However, Sierra Kunkaak has not extensively been explored botanically and it is a likely place for endemics. The lack of endemism on San Pedro Mártir may seem unusual as it is the most isolated island in the Gulf of California. However, with a hypothetical endemism of 5 percent, which would be comparable to that of San Pedro Nolasco, or San Clemente island off southern California, there would be only one endemic land plant on San Pedro Mártir. Furthermore, the genera to which the Gulf island endemics belong do not occur on San Pedro Mártir.

The positive relationship between the number of species on each island and island area is shown in Fig. 13. Figures 13 and 14 allow comparison of our floristic data with Soulé and Sloan's (1966) analysis of the biogeography of the terrestrial vertebrates of the Gulf of California (we treat several small islands which they do not, and we do not cover the Baja California islands which they do). In figure 13 "... the curve drawn ... between the highest points (the greatest species abun-

dance for their area) is a conservative estimate of the relationship between maximum species abundance and island area" (Soulé and Sloan 1966, p. 152). The percent saturation value given in figure 14 is the ratio of the actual number of species present on an island to a theoretical maximum predicted by the saturation curve.

Soulé and Sloan (1966, p. 151) report "... relative paucity of [terrestrial vertebrate] species on the deepwater, distant (from the mainland) islands." However, depauperate floras occur on the deepwater, isolated Isla San Pedro Mártir, as well as on the shallow-water Isla Patos and the scarcely isolated Isla Alcatraz. Although isolation seems to be a strong factor regulating species richness for certain of the Sonoran islands, it is well known that other factors such as habitat diversity are also highly significant in regulation of the size of insular biotas (for example see Hamilton, et al 1963). Some of the more obvious factors contributing to the regulation of species richness for the Sonoran islands are summarized below.

Isla Tiburón, scarcely isolated from the mainland, and with a high and complex topographic relief, is floristically a mainland "sample" of the flora rather than an island "isolate" (*sensu* Preston 1962). Thus Tiburón appears to be floristically saturated, retaining mainland species richness. Most striking are the impoverished floras on Islas San Pedro Mártir and Patos, and the exceedingly rich flora on Isla Dátil. Islas San Pedro Mártir and especially Patos have harsh environments, with relatively little habitat diversity, and extensive guano deposits which undoubtedly exert strong chemical control of the flora, preventing establishment of many species. Isla Alcatraz likewise has extensive guano deposits, and its flora is depauperate despite nearness to the mainland. Isla Dátil has the topography and microenvironments (see discussion on the islands above) which characteristically support maximum

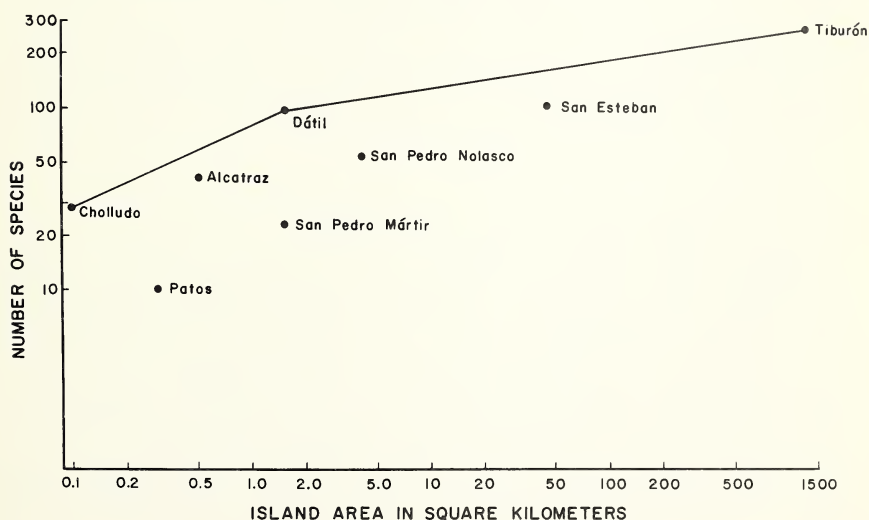


FIGURE 13. Species-area relationships of vascular plants on 8 islands on the eastern side of the Gulf of California. The line drawn through the upper points is a conservative "saturation curve" (see text).

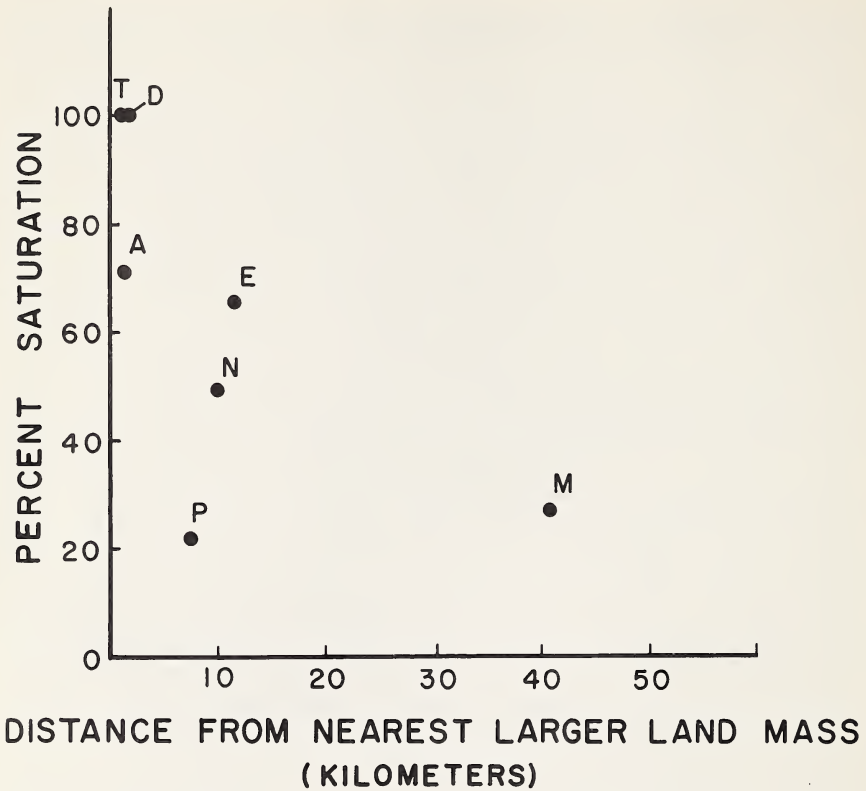


FIGURE 14. Percentage saturation of the floras on 8 islands on the eastern side of the Gulf of California (see Table 3). T=Tiburón, E=San Esteban, N=San Pedro Nolasco, M=San Pedro Mártir, D=Dátil (Turner's), A=Alcatraz, P=Patos, C=Cholludo.

species richness in the Gulf region, and its closeness to Isla Tiburón likewise contributes to the observed floristic richness.

Climatic variation among the smaller islands, and even on the different parts of Isla Tiburón, appear to be sufficient to influence species richness and floristic composition as well as vegetational aspects. For example we have observed that Islas Dátil and Cholludo, lying on the windward side of Sierra Kunkaak on Isla Tiburón, receive summer rains more often than do Islas Patos and Alcatraz, which are far more isolated from any mountain of sufficient mass to produce an orographic precipitation effect. However, there are no weather records for the islands.

Isla San Pedro Nolasco is nearly as complex topographically as Isla Dátil and is more than twice as large in area and more massive, yet it has a much smaller flora. This appears to be largely a function of the greater isolation of Nolasco than Dátil.

In summary, we consider island size, isolation, habitat diversity, aridity, and biotic factors such as absence or presence of mammalian herbivores and guano

deposits to be important factors controlling the evolution and distribution of the flora and vegetation of the islands in the Gulf of California.

CONSERVATION

The ecosystems of the islands in the Gulf of California remain mostly in a natural state. Development is accelerating and rapid environmental degradation is well underway throughout much of the region. Destruction of mangrove and other wetland coastal vegetation on the mainland is occurring at an alarming rate. Development in such areas needs to be contained and carefully planned; these unique tidal wetlands are essential to the continuation of the already threatened fisheries in the Gulf (Findley 1976). The great seabird rookery of Isla Raza has already received protection from the Mexican government. It is not too late for a realistic action plan to set aside the remaining uninhabited islands in the Gulf of California for natural wildlife or ecosystem reservations. This would result in no economic hardship and would be of great future value.

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RESUMEN

Se resumen flora y vegetación de las ocho islas mayores del lado oriental (Sonorense) del Golfo de California, con comentarios sobre la vegetación costera del Golfo en Sonora y Baja California. En orden de tamaño decreciente las islas estudiadas son Tiburón, San Esteban, San Pedro Nolasco, San Pedro Mártir, Dátil (Turner's), Alcatraz, Patos y Cholludo.

Se caracterizan y clasifican las comunidades vegetales mayores, a saber: *Pastizal de zacate marino*, *matorral del litoral* (manglares arbustivos y arbustos salados), *matorral desértico* (matorral costero, matorral de hediondilla, matorral desértico mixto, matorral de cactus, matorral desértico ribereño y aguajes o tinajas ribereñas) y *matorral espinoso* (matorral espinoso de los llanos, de piedemonte y ribereño).

En las mayores elevaciones de la parte Sur del Desierto Sonorense ocurren tres regiones disjuntas fundamentales de matorral espinoso: 1) sobre la Sierra de la Giganta, en el Sur de Baja California; 2) en la Sierra Kunkaak de la Isla Tiburón y; 3) en las montañas del Noroeste de Guaymas, en Sonora. La subdivisión que Shreve denomina *Piedemonte de Sonora* para este Desierto, se reclasifica como matorral espinoso en lugar de arbustal del desierto.

Se supone que las listas de plantas vasculares que se han dado para cada región están completas excepto en el caso de la Isla Tiburón para la cual estimamos conocer un 85 a 90%. Las cantidades de especies para cada una de las islas son las siguientes: Tiburón 286, San Esteban 107, San Pedro Nolasco 55, San Pedro Mártir 23, Dátil 99, Alcatraz 43, Patos 10 y Cholludo 28. Una novena isla, San Jorge, no tiene vegetación terrestre.

Son mayores las relaciones florísticas entre las islas del lado oriental del Golfo y Baja California que las de las islas del lado occidental y Sonora. Siete especies son endémicas en una o más islas del Golfo, (es decir, el 2, 1 por ciento de la flora de las ocho islas sonorenses). Solamente en la Isla San Pedro Nolasco ocurren endemismos únicos. En la Isla Tiburón, la más grande del Golfo de California, no se conocen plantas endémicas.

La relación positiva entre el área de la isla y el número de especies sufre considerables variaciones en las islas más pequeñas. El tamaño de las islas, el aislamiento, la diversidad topográfica y de habitat, la aridez, la presencia o ausencia de vertebrados herbívoros y los depósitos de guano parecen ser los factores principales que influyen sobre la evolución y distribución de la flora y vegetación de las islas del Golfo de California.

Sólo cuatro especies vegetales no nativas se han establecido en estas islas, lo que indica que tanto la acción del hombre antiguo como la del moderno tuvieron una mínima influencia sobre la biota natural. Esta es una situación rara en nuestros tiempos: la protección de los ecosistemas naturales de las islas del Golfo de California será de gran valor para el futuro.

TABLE 1
Distribution of Vascular Plants on Islas Tiburón, San Esteban, San Pedro Nolasco, San Pedro Mártir, Dátil, Alcatraz, and Cholludo

	Tiburón	San Esteban	San Pedro Nolasco	San Pedro Mártir	Dátil (=Turner's)	Alcatraz	Cholludo	Community ⁴ (commonest occurrence)
Lycopsidea								
<i>Selaginellaceae</i>								
<i>Selaginella arizonica</i> Maxon	T ⁵							TS ?
Filices								
<i>Pteridaceae</i>								
<i>Cheilanthes wrightii</i> Hook.	T							RD
<i>Notholaena californica</i> D.C. Eaton	T							MX, RD
<i>N. lemmonii</i> D.C. Eaton				N				MX
Gnetae								
<i>Ephedraceae</i>								
<i>Ephedra aspera</i> Engelm. ex S. Wats.		E						MX
Dicotyledoneae Angiospermae ⁶								
<i>Acanthaceae</i>								
<i>Beloperone californica</i> Brandeg.	T	E				A	C	RD, MX
<i>Berginia virgata</i> Harv. ex. Benth. & Hook. var. <i>virgata</i>	T				D			MX, RD, TS
<i>Carlownrightia arizonica</i> A. Gray	T	E			D			MD, RD
<i>Dicliptera resupinata</i> (Vahl) Juss.	T							RD
<i>Elytraria imbricata</i> (Vahl) Pers.	T							RD, TS
<i>Jacobinia ovata</i> A. Gray var. <i>ovata</i>	T							RD, TS
<i>Ruellia californica</i> (Rose) I.M. Johnston.	T							MX, RD, TS
<i>Siphonoglossa longiflora</i> (Torr.) A. Gray	T							MX, RD, TS

TABLE 1 (cont'd)

	Tiburón	San Esteban	San Pedro Nolasco	San Pedro Mártir	Dátil (=Turner's)	Alcatraz	Cholludo	Community ¹ (commonest occurrence)
<i>Aizoaceae</i>								
<i>Mollugo cerviana</i> (L.) Ser.	T							CR, MX
<i>M. verticillata</i> L.			N					MX
<i>Sesuvium verrucosum</i> Raf.	T					A		SS
<i>Trianthema portulacastrum</i> L.	T					A		CR, MX, RD
<i>Amaranthaceae</i>								
<i>Amaranthus fimbriatus</i> (Torr.) Benth. ex S. Wats.	T		N		D	A		MX, RD, TS
<i>A. watsonii</i> Standl.	T	E			D	A		MX, RD
<i>Tidestromia lanuginosa</i> (Nutt.) Standl.	T							MX, RD, TS
<i>Apocynaceae</i> (incl. <i>Asclepiadaceae</i>)								
<i>Asclepias albicans</i> S. Wats.	T	E			D			MX
<i>A. subulata</i> Dene. in A. DC.	T							MX
<i>Haplophyton cemicidum</i> A. DC. var. <i>crooksii</i> L. Bens.	T							RD, TS
<i>Marsdenia edulis</i> S. Wats.	T							RD, TS
<i>Matelea pringlei</i> (A. Gray) Woods.	T							MX, RD
<i>M. cordifolia</i> (A. Gray) Woods.	T							RD
<i>Metastelma pringlei</i> A. Gray			N					MX
<i>Vallesia glabra</i> (Cav.) Link var. <i>glabra</i>	T							RD
<i>Araliaceae</i> (incl. <i>Apiaceae</i>)								
<i>Daucus pusillus</i> Michx.	T							MX, RD

TABLE 1 (cont'd)

	Tiburón	San Esteban	San Pedro Nolasco	San Pedro Mártir	Dátil (=Turner's)	Alcatraz	Cholludo	Community [†] (commonest occurrence)
<i>Helianthus niveus</i> (Benth.) Brandeg. cf. <i>ssp. tephrodes</i> (Gray) Heiser	T							CO
<i>Hofmeisteria crassifolia</i> S. Wats.			N					MX, CS
<i>H. fasciculata</i> (Benth.) Walp. var. <i>fasciculata</i>	T	E			D		C	MX, CS
<i>Hymenoclea monogyra</i> T. & G.	T							RD
<i>H. pentalepis</i> Rydb.	T							RD
<i>Palafoxia arida</i> Turner & Morris var. <i>arida</i>	T					A		CO, MX
<i>Pectis palmeri</i> S. Wats.	T						C	RD, MX, CS
<i>P. papposa</i> Harv. & Gray var. <i>papposa</i>	T							CR, MX, RD
<i>Pelucha trifida</i> S. Wats.	T			M				MX, CS
<i>Perityle aurea</i> Rose	T							MX, RD
<i>P. cf. aurea</i> Rose		E						MX, RD
<i>P. californica</i> Benth.			N					MX, RD
<i>P. emoryi</i> Torr.	T	E	N	M	D	A	C	MX, RD, CR, CS
<i>Peucephyllum schottii</i> (A. Gray) A. Gray		E						MX
<i>Pleurocornis laphamiodes</i> (Rose) King & Robins.	T	E	N	M	D	A		MX, CS
<i>Porophyllum crassifolium</i> S. Wats.	T	E			D			SS, MX
<i>P. gracile</i> Benth.	T	E			D			MX, RD
<i>P. pausodunum</i> Robins. & Greenm.			N					MX

<i>Trixis californica</i> Kell. var. <i>californica</i>	T	E	N	M	D	MX, RD, TS
<i>Verbesina palmeri</i> S. Wats. ssp. <i>oligocephala</i> (I. M. Johnst.) Felger & Lowe	T					MX, TS
<i>Viguiera deltoidea</i> A. Gray var. <i>chenopodiina</i> (Greene) S. F. Blake	T		N	M	D	MX, RD
<i>V. deltoidea</i> var. <i>parishii</i> (Greene) Vasey & Rose		E				MX, RD
<i>Bataceae</i>						
<i>Batis maritima</i> L.	T					MS, SS
<i>Boraginaceae</i>						
<i>Coldenia canescens</i> DC.					D	MX CO
<i>C. palmeri</i> A. Gray	T					MX, CR
<i>Cordia parvifolia</i> A. DC.	T					MX
<i>Cryptantha angelica</i> I. M. Johnst.	T					CR, MX, RD
<i>C. angustifolia</i> (Torr.) Greene	T	E				MX, RD, TS
<i>C. fastigiata</i> I. M. Johnst.	T	E			D	CR, MD, RD
<i>C. maritima</i> (Greene) Greene	T	E				RA, SS
<i>Heliotropium curassavicum</i> L.	T					RA
<i>Tournefortia hartwegiana</i> Steud.	T					
<i>Brassicaceae</i>						
<i>Descurainia pinnata</i> (Walt.) Britt. ssp. <i>hallerorum</i> (Cockerell) Detl.	T	E			D	MX, RD
<i>Draba cuneifolia</i> Nutt. ex. T. & G. var. <i>sonorae</i> (Greene) Parish	T	E			D	MX, RD
<i>Lyrocarpa coulteri</i> Hook. & Harv. ex Harv. var. <i>coulteri</i>	T				D	MX, RD

TABLE 1 (cont'd)

	Tiburón	San Esteban	San Pedro Nolasco	San Pedro Martir	Dátil (=Turner's)	Alcatraz	Cholludo	Community ¹ (commonest occurrence)
<i>L. linearifolia</i> Roll. in Gentry		E						RD
unidentified winter ephemeral	T							RD
<i>Burseraceae</i>								
<i>Bursera hindsiana</i> (Benth.) Engler	T	E			D		C	MX, RD
<i>B. laxiflora</i> S. Wats. ssp. <i>laxiflora</i>	T							MX, TS
<i>B. microphylla</i> A. Gray	T	E	N		D	A		MX, RD
<i>Buxaceae</i> (see Simmondsiaceae)								
<i>Cactaceae</i>								
<i>Carnegiea gigantea</i> (Engelm.) Britt. & Rose	T					A	C	MX, DS
<i>Echinocereus grandis</i> Britt. & Rose		E						MX
<i>E. websterianus</i> Lindsay			N					MX, CS
<i>E. pectinatus</i> (Scheidw.) Engelm. var. <i>scopulorum</i> (Britt. & Rose) L. Bens.	T							MX
<i>Ferocactus wislizenii</i> (Engelm.) Britt. & Rose var. <i>tiburonensis</i> Lindsay	T							MX
<i>Lemaireocereus thurberi</i> (Engelm.) Britt. & Rose	T	E	N	— ⁷	D	A	C	MX, CS, TS
<i>Lophocereus schottii</i> (Engelm.) Britt. & Rose var. <i>schottii</i>	T	E ⁸			D	A	C	MX, CS
<i>Machaerocereus gummosus</i> (Engelm.) Britt. & Rose	T	E			D		C	MX, CS, CO
<i>Mammillaria dioeca</i> K. Brandeg. sp. ?					D		C	MX, CS
<i>M. estebanensis</i> Lindsay		E						MX

<i>M. microcarpa</i> Engelm.	T				A	MX
<i>M. multidentata</i> W. T. Marshall			N			MX, CS
<i>M. taylortorum</i> Glass & Foster			N			MX, CS
<i>Opuntia bigelovii</i> Engelm. var. <i>bigelovii</i>	T	E			D	MX
<i>O. ciribe</i> Engelm. ex Coult.		E				MX
<i>O. fulgida</i> Engelm. var. <i>fulgida</i>	T			M	A	MX, CS
<i>O. fulgida</i> var. <i>mammillata</i> (Schott ex Engelm.) Coult.	T		N		D	MX, CS, CO
<i>O. leptocaulis</i> DC.	T				D	MX
<i>O. phaeacantha</i> Engelm. var. <i>discata</i> (Griff.) Bens. & Walk.					A	MX
<i>O. wilcoxii</i> Britt. & Rose			N			MX
<i>O. thurberi</i> Engelm. ssp. <i>versicolor</i> (Engelm. ex Coult.) Felger & Lowe	T				D	MX, CS, TS
<i>Neoevansia striata</i> (Brandeg.) Sanch. Mejor.	T				D	MX, CS
<i>Pachycereus pringlei</i> (S. Wats.) Britt. & Rose	T	E	N	M	D	MX
<i>Campanulaceae</i>						
<i>Nemacladus glanduliferus</i> Jeps. var. <i>glanduliferus</i>		E			D	RD
<i>Capparaceae</i>						
<i>Atamisquea emarginata</i> Miers	T	E			C	MX, CS
<i>Cleome tenuis</i> S. Wats.	T					MX, RD
<i>Caryophyllaceae</i>						
<i>Achyronychia cooperi</i> A. Gray	T					CO, CR, MX
<i>Drymaria holosteoides</i> Benth.	T					CR, MX

TABLE 1 (cont'd)

	Tiburón	San Esteban	San Pedro Nolasco	San Pedro Mártir	Dátil (= Turner's)	Alcatraz	Cholludo	Community ⁴ (commonest occurrence)
<i>Celastraceae</i>								
<i>Tricerna phyllanthoides</i> (Benth.) Lundell	T					A		MS, SS, RD
<i>Chenopodiaceae</i>								
<i>Allenrolfea occidentalis</i> (S. Wats.) Kuntze	T					A		SS
<i>Atriplex barclayana</i> (Benth.) Dietr.	T	E			D	A	C	SS, CO, CS, MX
<i>A. linearis</i> S. Wats.	T							CO, MX
<i>A. polycarpa</i> (Torr.) S. Wats.	T	E			D			MX, RD
<i>Chenopodium murale</i> L.	T					A		CO, MX
<i>Salicornia europea</i> L.	T							MS, SS
<i>S. virginica</i> L.	T							SS
<i>Suaeda torreyana</i> S. Wats.	T	E			D	A		SS
<i>Suaeda</i> sp.	T							SS
<i>Combretaceae</i>								
<i>Laguncularia racemosa</i> (L.) Gaertn. f.	T							MS
<i>Convolvulaceae</i>								
<i>Cressa truxillensis</i> HBK.	T					A		SS
<i>Cuscuta leptantha</i> Engelm.	T				D			MX
<i>C. corymbosa</i> Ruiz & Pav. var. <i>grandiflora</i> Engelm.		E	N					MX
<i>Cuscuta</i> sp.	T							MX
<i>Evolvulus alsinoides</i> L. var. <i>acapulcensis</i> (Willd.) Oosttr.	T							MX, TS, RD

<i>Jacquemontia abutiloides</i> Benth. var. eastwoodiana (I. M. Johnston.) Wigg.	T					RD, MX
<i>Ipomoea</i> sp.	T					RD, MX
<i>Cucurbitaceae</i>						
<i>Maximowiczia sonora</i> S. Wats. var. <i>sonora</i>	T					RD
<i>Vaseyanthus insularis</i> Rose & vars.	T	E	N	M		MX
<i>Euphorbiaceae</i>						
<i>Acalypha californica</i> Benth.	T	E			D	MX, RD, TS
<i>A. comondwana</i> Millsp.	T					RD, TS
<i>Andrachne ciliato-glandulosa</i> (Millsp.) Croizat	T					MX, RD
<i>Bemardia cinerea</i> Wigg. & Roll.			N			MX
<i>Cnidioscolus palmeri</i> (S. Wats.) Rose	T ^{5,9}				D	MX, RD
<i>Croton californicus</i> Muell. Arg. var. <i>californicus</i>	T					CO, MX
<i>C. magdalenae</i> Millsp.	T					RD, TS
<i>C. sonora</i> Torr.	T					MX, RD, TS
<i>Ditaxis lanceolata</i> (Benth.) Pax & Hoffm.	T	E			D	MX, RD
<i>D. serrata</i> (Torr.) Heller	T	E			D	MX, CR, RD
<i>Euphorbia arizonica</i> Engelm.	T					MX, RD
<i>E. eriantha</i> Benth.	T					MX, RD
<i>E. florida</i> Engelm.	T					MX, RD
<i>E. leucophylla</i> Benth.	T					CO
<i>E. magdalenae</i> Benth.	T		N			MX

TABLE 1 (cont'd)

	Tiburón	San Esteban	San Pedro Nolasco	San Pedro Mártir	Dátil (=Turner's)	Alcatraz	Cholludo	Community ⁴ (commonest occurrence)
<i>E. misera</i> Benth.	T	E			D			MX
<i>E. pediculifera</i> Engelm.	T	E			D			MX
<i>E. petrina</i> S. Wats.	T	E		M		A		MX, CO
<i>E. polycarpa</i> Benth. var. <i>hirtella</i> Boiss.	T	E			D			MX
<i>E. polycarpa</i> var. <i>polycarpa</i>	T							MX
<i>E. setiloba</i> Engelm.	T	E						MX, RD, CR
<i>E. tomentulosa</i> S. Wats.	T							MX
<i>Jatropha cinerea</i> (Ortega) Muell. Arg.	T							MX
<i>J. cuneata</i> Wigg. & Roll.	T	E	N		D			MX
<i>Pedilanthus macrocarpus</i> Benth.			N					MX
<i>Sapium biloculare</i> (S. Wats.) Pax	T							MX, RD
<i>Tragia amblyodonta</i> (Muell. Arg.) Pax & Hoffm.	T				D			RD
<i>Fabaceae</i>								
<i>Acacia greggii</i> A. Gray	T							RD
<i>A. willardiana</i> Rose	T		N					MX, RD
<i>Calliandra californica</i> Benth.								RD, MX
<i>C. eriophylla</i> Benth.	T				D			MX, RD
<i>C. schottii</i> Torr. ex S. Wats. ssp. <i>rosei</i> (Wigg.) Felger & Lowe	T							RD, TS
<i>Cassia confinis</i> Greene	T							MX

<i>C. covesii</i> A. Gray	T	E		D	MX, CR
<i>Cercidium floridum</i> Benth. ex A. Gray ssp. <i>floridum</i>	T				RD
<i>C. microphyllum</i> (Torr.) Rose & Johnst.	T	E			MX, RD
<i>Coursetia glandulosa</i> A. Gray	T				RD, TS
<i>Dalea emoryi</i> A. Gray	T				MX, CO
<i>D. mollis</i> Benth.	T			A	MX, CR
<i>D. parryi</i> (A. Gray) T. & G	T	E		D	MX
<i>D. vetula</i> Brandeg.	T				MX
<i>Desmanthus covillei</i> (Britt. & Rose) Wigg. ex Turner	T				RD, TS
<i>D. fruticosus</i> Rose	T	E		D	RD, MX
<i>Errazurizia megacarpa</i> (S. Wats.) I.M. Johnst.	T				CO, MX
<i>Hoffmanseggia intricata</i> Brandeg.	T	E		D	MX
<i>Lotus salsuginosus</i> Greene ssp. <i>brevivexillus</i> (Ottley) Munz	T				MX, CR
<i>L. tomentellus</i> Greene	T	E			MX, CR
<i>Lupinus</i> cf. <i>arizonicus</i> S. Wats.	T	E			MX, RD
<i>Lysiloma divaricata</i> (Jacq.) J. F. Macbr.	T				RD, TS
<i>Mimosa laxiflora</i> Benth. in Hook.	T				RD, MX
<i>Olneya tesota</i> A. Gray	T	E		A	RD, MX
<i>Phaseolus filiformis</i> Benth.	T	E		D	RD, MX
<i>Phaseolus</i> sp.	T ^{5,9}				RD, MX
<i>Pithecellobium confine</i> Standl.	T			D	MX, RD

TABLE 1 (cont'd)

	Tiburón	San Esteban	San Pedro Nolasco	San Pedro Mártir	Dátil (=Turner's)	Alcatraz	Cholludo	Community ⁴ (commonest occurrence)
<i>Prosopis glandulosa</i> Torr. var. torreyana (Benson) M.C. Johnst.	T	E			D	A		RD, MX
<i>Tephrosia palmeri</i> S. Wats.	T							MX
<i>Fouquieriaceae</i>								
<i>Fouquieria diguetii</i> (Van Tiegh.) I. M. Johnst.		— ¹⁰	N					MX
<i>F. splendens</i> Engelm. ssp. <i>splendens</i>	T				D			MX, CO
<i>Frankeniaceae</i>								
<i>Frankenia palmeri</i> S. Wats.	T							CO
<i>Hydrophyllaceae</i>								
<i>Eucrypta micrantha</i> (Torr.) Heller	T							RD, MX
<i>Nama hispidum</i> A. Gray	T							MX, CR, RD
<i>Phacelia minutiflora</i> J. W. Voss ex Munz	T							MX
<i>P. crenulata</i> A. Gray	T	E						MX, RD
<i>P. pedicellata</i> A. Gray	T	E			D			MX, RD
<i>Koeberliniaceae</i>								
<i>Koeberlinia spinosa</i> Zucc.	T							MX, RD
<i>Krameriaceae</i>								
<i>Krameria grayi</i> Rose & Painter	T							MX, CR
<i>K. parvifolia</i> Benth.	T							MX
<i>Lamiaceae (Labiatae)</i>								
<i>Hyptis emoryi</i> Torr.	T	E			D			RD, MX
<i>Salvia similis</i> Brandeg.			N					MX

<i>Loasaceae</i>					
<i>Eucnide cordata</i> Kell. ex Curran	E				MX
<i>E. rupestris</i> (Baill.) Thomps. & Ernst	T		N	D	MX, CS
<i>Mentzelia adhaerans</i> Benth.	T		N	D	MX, CS, CR, RD
<i>M. hirsutissima</i> S. Wats.	T				MX
<i>Petalonyx linearis</i> Greene	T		M		MX
<i>Malpigiaceae</i>					
<i>Janusia californica</i> Benth.	T			D	RD, TS, MX
<i>J. gracilis</i> A. Gray	T			D	MX, RD
<i>Mascagnia macroptera</i> (Sessé & Moc.) Nieden.	T				RD, TS
<i>Thryallis angustifolia</i> (Benth.) Kuntze	T	N			MX
<i>Mahvaceae</i>					
<i>Abutilon californicum</i> Benth.	T				RD, MX
<i>A. crispum</i> Sweet	T			D	MX, RD
<i>A. incanum</i> (Link) Sweet ssp. <i>incanum</i>	T			D	MX, RD
<i>A. palmeri</i> A. Gray	T		M		RD
<i>Gossypium klotzschianum</i> Anders. var. <i>dauidsonii</i> (Kell.) J. B. Hutch.			N		MX
<i>Hibiscus bisepetus</i> S. Wats.	T				MX
<i>H. denudatus</i> Benth.	T	E		D	MX
<i>Horsfordia alata</i> (S. Wats.) A. Gray	T				RD
<i>H. newberryi</i> (S. Wats.) A. Gray	T	E			RD, MX
<i>Sphaeralcea ambigua</i> A. Gray var. <i>ambigua</i>	T			D	MX

TABLE 1 (cont'd)

	Tiburón	San Esteban	San Pedro Nolasco	San Pedro Mártir	Dátil (=Turner's)	Alcatraz	Cholludo	Community ⁴ (commonest occurrence)
<i>S. ambigua</i> var. <i>versicolor</i> (Kearney) Kearney		E						MX
<i>S. hainesii</i> Brandege				M				MX
<i>S. orcuttii</i> Rose	?					A		MX
<i>Martyniaceae</i>								
<i>Proboscidea altheaeifolia</i> (Benth.) Dcne.	T							MX, RD
<i>Moraceae</i>								
<i>Ficus petiolaris</i> HKB, ssp. <i>palmeri</i> (S. Wats.) Felger & Lowe	T	E	N	M	D	A	C	RD, MX, CS, TS
<i>Nyctaginaceae</i>								
<i>Abronia maritima</i> Nutt. ex S. Wats.	T					A		SS
<i>Allionia incarnata</i> L.	T				D			MX, CR
<i>Boerhaavia coulteri</i> (Hook f.) S. Wats.	T	E						MX, RD
<i>B. erecta</i> L.	T						D	MX, RD
<i>Boerhaavia</i> sp.			N					MX
<i>Commicarpus scandens</i> (L.) Standl.	T							RD, MX
<i>Mirabilis tenuiloba</i> S. Wats.		E						MX
<i>Onagraceae</i>								
<i>Camissonia californica</i> (Nutt. ex T. & G.) Raven	T							MX, RD
<i>C. cardiophylla</i> (Torr.) Raven ssp. <i>cardiophylla</i>	T	E		M				MX
<i>C. chamaenerioides</i> (A. Gray) Raven	T							MX, RD

<i>Oenothera californica</i> S. Wats. ssp. arizonica (Munz) Klein	T					CO, MX
<i>Papaveraceae</i>						
<i>Argemone subintegrifolia</i> Ownby		E				MX
<i>Eschscholzia minutiflora</i> S. Wats.	T					MX
<i>Passifloraceae</i>						
<i>Passiflora arida</i> (Mast. & Rose) Killip var. arida	T	E				MX, RD
<i>P. palmeri</i> Rose	T	E			D	MX, RD
<i>Phytolaccaceae</i>						
<i>Phaulothamnus spinescens</i> A. Gray	T		N		D	MX, RD, CS
<i>Stegnosperma halimifolium</i> Benth.	T	E		M	D	MX, RD, CS
<i>Plumbaginaceae</i>						
<i>Plumbago scandens</i> L.	T					RD, TS
<i>Polygonaceae</i>						
<i>Eriogonum inflatum</i> Torr. & Frem.	T	E				MX
<i>Portulacaceae</i>						
<i>Portulaca lanceolata</i> Engelm. & Gray	T					MX
<i>P. parvula</i> A. Gray	T					MX
<i>Portulaca</i> sp.	T					MX
<i>Resedaceae</i>						
<i>Oligomeris linifolia</i> (Vahl) Macbr.	T	E			D	MX, CR
<i>Rhamnaceae</i>						
<i>Colubrina viridis</i> (Jones) M. C. Johnst.	T	E	N		D	MX, RD, CS
<i>Condalia globosa</i> I. M. Johnst. var. pubescens I. M. Johnst.	T	E			D	MX, RD
<i>Zizyphus obtusilobus</i> (T. & G.) A. Gray var. canescens (Gray) M. C. Johnst.	T	E			D	RD, MX

TABLE 1 (cont'd)

	Tiburón	San Esteban	San Pedro Nolasco	San Pedro Mártir	Dátil (=Turner's)	Alcatraz	Cholludo	Community ⁴ (commonest occurrence)
<i>Rhizophoraceae</i>								
<i>Rhizophora mangle</i> L.	T							MS
<i>Rubiaceae</i>								
<i>Randia thurberi</i> S. Wats.	T							MX, RD, TS
<i>Salicaceae</i>								
<i>Salix gooddingii</i> Ball. var. <i>gooddingii</i>	T							RA
<i>Sapindaceae</i>								
<i>Cardiospermum corindum</i> L.	T				D			MX, RD RD, MX
<i>Dodonaea viscosa</i> Jacq.	T							RD
<i>Sapotaceae</i>								
<i>Bumelia occidentalis</i> Hemsl.	T							MX, RD
<i>Sideroxylon leucophyllum</i> S. Wats		E						MX, RD
<i>Scrophulariaceae</i>								
<i>Antirrhinum cyathiferum</i> Benth.	T	E	N		D		C	MX, RD CS, CR
<i>A. kingii</i> S. Wats. var. <i>watsonii</i> (Vasey & Rose) Munz	T				D			MX, RD
<i>Galvezia juncea</i> (Benth.) Ball var. <i>pubescens</i> (Brandeg.) I. M. Johnston.		E	N					RD, MX
<i>Linaria canadensis</i> (L.) Dum-Cours. var. <i>texana</i> (Scheele) Penn.	T							RA
<i>Stemodia durantifolia</i> (L.) Sw.	T							RA
<i>Simaroubaceae</i>								
<i>Castela polyandra</i> Moran & Felger	T							MX

<i>Simmondsiaceae</i>							
<i>Simmondsia chinensis</i> (Link) Schneid.	T	E	N	D			MX, RD
<i>Solanaceae</i>							
<i>Datura discolor</i> Benth.	T			D	A		MX, RD
<i>Lycium andersonii</i> A. Gray var. <i>andersonii</i>	T	E					RD, MX
<i>L. andersonii</i> var. <i>deserticola</i> (Hitchc.) Jeps.	T						RD, MX
<i>L. brevipes</i> Benth. var. <i>brevipes</i>	T	E		M	A	C	CS, MX, RD
<i>L. californicum</i> Nutt. ex Gray ssp. <i>californicum</i>	T						CO, MX
<i>L. fremontii</i> A. Gray var. <i>fremontii</i>	T						MX, RD
<i>L. megacarpum</i> Wigg.		E					MX
<i>Nicotiana clevelandii</i> A. Gray	T						MX, RD
<i>N. trigonophylla</i> Dunal	T	E		M	A	C	MX, RD, CS
<i>Physalis crassifolia</i> Benth. var. <i>versicolor</i> (Rydb.) Waterfall	T						MX
<i>P. crassifolia</i> var. <i>infundibularis</i> I. M. Johnston.		E					MX
<i>P. pubescens</i> L.	T						RA
<i>Solanum hindsianum</i> Benth.	T	E		D			MX, RD
<i>Sterculiaceae</i>							
<i>Ayenia compacta</i> Rose	T	E					MX
<i>A. glabra</i> S. Wats.	T						RD, TS
<i>Melochia tomentosa</i> L. var. <i>tomentosa</i>	T		N	D			MX, RD
<i>Tamaricaceae</i>							
<i>Tamarix ramosissima</i> Ladeb	T						RA

TABLE 1 (cont'd)

	Tiburón	San Esteban	San Pedro Nolasco	San Pedro Mártir	Dátil (=Turner's)	Alcatraz	Cholludo	Community ⁴ (commonest occurrence)
<i>Theophrastaceae</i>								
<i>Jacquinia pungens</i> A. Gray	T							MX, RD
<i>Ulmaceae</i>								
<i>Celtis pallida</i> Torr.	T							RD, MX
<i>Urticaceae</i>								
<i>Parietaria floridana</i> Nutt.	T	E	N		D			RD, MX
<i>Verbenaceae</i>								
<i>Avicennia germinans</i> (L.) Stearn	T							MS
<i>Lippia palmeri</i> S. Wats.	T				D			MX, RD
<i>Violaceae</i>								
<i>Hybanthus fruticosus</i> (Benth.) I. M. Johnston. var. <i>flavescens</i> (Dow.) I. M. Johnston.	T							RD, MX
<i>Viscaceae</i>								
<i>Phoradendron californicum</i> Nutt.	T							MX, RD
<i>P. diguetianum</i> Van Tiegh.	T							MX, CR, MS
<i>Zygophyllaceae</i>								
<i>Fagonia californica</i> Benth.	T				D			MX
<i>F. pachyacantha</i> Rydb. in Vail & Rydb.	T							MX, CR
<i>F. palmeri</i> Vasey & Rose	T							MX
<i>Guaiacum coulteri</i> A. Gray	T							RD, TS
<i>Kallstroemia californica</i> (S. Wats.) Vail var. <i>brachystylis</i> (Vail) Kearns. & Peebl.	T				D			MX, CR, RD
<i>K. grandiflora</i> Torr. ex A. Gray	T							MX, CR, RD

<i>Larrea divaricata</i> Cav. ssp. tridentata (Sessé & Moc. ex DC.) Felger & Lowe	T								CR, MX
<i>Viscainoa geniculata</i> (Kell.) Greene var. <i>geniculata</i>	T	E	M	D	A	C			MX, CS
Monocotyledoneae									
<i>Cyperaceae</i>									
<i>Cyperus aristatus</i> Rothb.			M						MX
<i>C. elegans</i> L.	T								RA
<i>Eleocharis geniculata</i> (L.) R. & S.	T								RA
<i>Liliaceae</i>									
<i>Agave chrysglossa</i> I. M. Johnst.	T		N						MX
<i>A. dentiens</i> Trel.		E							MX
<i>A. subsimplex</i> Trel.	T			D		C			MX
<i>Poaceae</i>									
<i>Aristida adscensionis</i> L.	T	E	N	D					MX, CR, RD
<i>A. californica</i> Thurb. ex S. Wats.	T								CO, MX
<i>A. ternipes</i> Cav.	T		N						MX
<i>A. wrightii</i> Nash	T								MX
<i>Bothriochloa barbinodis</i> (Lag.) Herter			N						MX
<i>Bouteloua aristoides</i> (HBK.) Griseb.	T	E	N	D	A	C			MX, CR, CS
<i>B. barbata</i> Lag.	T	E			A				MX, CR
<i>Catastecum erectum</i> Vasey & Hack.	T								MX, RD, TS
<i>Cenchrus palmeri</i> Vasey	T	E	N		A				CO, MX
<i>Chloris brandegeei</i> (Vasey) Swallen		E							MX, RD
<i>Distichlis spicata</i> (L.) Greene var. <i>stricta</i> (Gray) Beetle	T								RA

TABLE 1 (cont'd)

	Tiburón	San Esteban	San Pedro Nolasco	San Pedro Mártir	Dátil (=Turner's)	Alcatraz	Cholludo	Community ⁴ (commonest occurrence)
<i>Eragrostis diffusa</i> Buck.			N					MX
<i>Erioneuron pulchellum</i> (HBK.) Tateoka	T	E			D			MX
<i>Heteropogon contortus</i> (L.) Beauv. ex R. & S.	T	E						MX, RD
<i>Lasiacis sorghoides</i> (Desv.) Hitch. & Chase	T							RA
<i>Leptochloa filiformis</i> Beauv. var. <i>filiformis</i>	T		N					MX, RD, TS
<i>Monanthochloe littoralis</i> Engelm.	T					A		SS
<i>Muhlenbergia microsperma</i> (DC.) Kunth	T	E	N	M			C	MX, RD, TS
<i>Panicum</i> cf. <i>arizonicum</i> Scribn. & Merr.	T	E			D		C	MX, RD
<i>P. capillare</i> L. var. <i>hirticaule</i> (Presl.) Gould	T							RD, TS
<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	T							RA
<i>Setaria liebmannii</i> Fourn.	T							MX, RD
<i>S. macrostachya</i> HBK.	T	E	N		D			MX, RD
<i>Sporobolus cryptandrus</i> (Torr.) A. Gray	T							CO, MX
<i>S. patens</i> Swall.	T							MX, RD
<i>S. virginicus</i> (L.) Kunth	?					A		SS
<i>Trichachne californica</i> (Benth.) Chase	T		N		D		C	MX
<i>Trichloris crinata</i> (Lag.) Parodi			N					MX
<i>Potamogetonaceae</i>								
<i>Ruppia maritima</i> L.	T							SG

<i>Typhaceae</i>			
<i>Typha domingensis</i> Pers.	T		RA
<i>Zosteraceae</i>			
<i>Zostera marina</i> L.	T	A ¹¹	SG

4. SG = seagrass meadow, MS = mangrove scrub, SS = saltscrub, CO = coast scrub, CR = creosotebush scrub, MX = mixed desertscrub, CS = cactus scrub, RD = riparian desertscrub, RA = riparian *aguaje*, TS = thornscrub and desertscrub-thornscrub ecotone.
5. Presence verified by Seri Indian informants (see Felger and Moser 1970, etc., and unpublished data). We consider these reports to be highly reliable.
6. Family designations follow Thorne (1968).
7. *Lemnaceae* is reported on San Pedro Mártir by Gentry (1949) and Hastings et al. (1972). This seems to be an error. Neither Reid Moran nor I have found it there.
8. We have not found *Lophocereus* on San Esteban. The report of its occurrence on that island by Hastings et al. (1972) is based on a specimen from that island collected by D. Bostic (SD).
9. Felger and Moser (1976).
10. *Fouquieria diguetii* does not seem to occur on San Esteban, although Gentry (1949) and Hastings et al. (1972) report it is (was) there, and Johnston (1924) infers it was present. Concerning San Esteban and this species, Reid Moran (*personal communication*) says "I have not collected it, do not recollect seeing it, and do not find it listed in my field notes."
11. In beach drift, and probably not growing close offshore from this island.

Abutilon 4
Aristida 4
Cryptantha 4
Dalea 4

The 8 Islands:							
	Number	Percent		Number	Percent		
Asteraceae	22 (33)	10.1 (10.1)	Solanaceae	5 (10)	2.3 (3.1)		
Fabaceae	18 (29)	8.3 (8.9)	Acanthaceae	8 (8)	3.7 (2.4)		
Poaceae	20 (28)	9.2 (8.6)	Boraginaceae	5 (9)	2.3 (2.8)		
Euphorbiaceae	11 (26)	5.1 (8.0)	Chenopodiaceae	5 (9)	2.3 (2.8)		
Cactaceae	10 (22)	4.6 (6.7)	Apocynaceae	6 (8)	2.8 (2.4)		
Malvaceae	5 (12)	2.3 (3.7)					
Tiburón:							
Asteraceae	21 (28)	10.4 (9.8)	Malvaceae	4 (10)	2.0 (3.5)		
Fabaceae	18 (28)	9.0 (9.8)	Chenopodiaceae	5 (9)	2.5 (3.2)		
Poaceae	16 (24)	8.0 (8.4)	Acanthaceae	8 (8)	4.0 (2.8)		
Euphorbiaceae	9 (24)	4.5 (8.4)	Boraginaceae	5 (8)	2.5 (2.8)		
Cactaceae	10 (13)	5.0 (4.6)	Apocynaceae	5 (7)	2.5 (2.5)		
Solanaceae	5 (10)	2.5 (3.5)					
San Esteban:							
Asteraceae	12 (14)	13.3 (13.2)	Solanaceae	4 (5)	4.4 (4.7)		
Fabaceae	10 (10)	11.1 (9.4)	Malvaceae	3 (3)	3.3 (2.8)		
Poaceae	9 (10)	10.0 (9.4)					
Euphorbiaceae	4 (9)	4.4 (8.5)					
Cactaceae	6 (7)	6.7 (6.6)					
San Pedro Nolasco:							
Poaceae	10 (11)	19.6 (20.0)					
Asteraceae	8 (9)	15.7 (16.4)					
Cactaceae	5 (7)	9.8 (12.7)					
Euphorbiaceae	4 (4)	7.8 (7.3)					

TABLE 2 (cont'd)
Largest Families (General & Species)

Dátil:	<i>Number</i>	<i>Percent</i>
Asteraceae	10 (11)	11.6 (11.3)
Cactaceae	7 (10)	8.1 (10.3)
Fabaceae	9 (9)	10.5 (9.3)
Euphorbiaceae	6 (9)	7.0 (9.3)
Poaceae	6 (6)	7.0 (6.2)

TABLE 3
Geographic Data for the Sonoran Islands

Island	Area (km²)	Nearest larger land Mass and distance	Highest Elevation	Number of Species
Tiburón	ca 1210	Punta Santa Rosa, Sonora 1.4 km	875	286
San Esteban	43	South shore Tiburón 11.6 km	550	107
San Pedro Nolasco	3.5	Punta San Pedro, Sonora 10.0 km	318	55
San Pedro Mártir	1.5 +	Punta Monumento, south shore Tiburón 40.7 km	320	23
Dátil	1.5	Punta Monumento, south shore Tiburón 1.9 km	183	99
Alcatraz	0.5	Bahía Kino, Sonora 1.4 km	130	43
Patos	0.3	Northwest shore Tiburón 7.3 km	69	10
Cholludo	ca 0.1	North shore Dátil ca 0.5 km	ca 75 +	28

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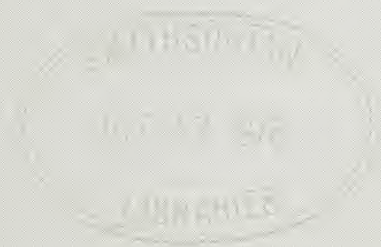
OCTOBER 19, 1976

THE STATUS OF
CALIFORNIA AND ARIZONA POPULATIONS OF THE WESTERN
SPADEFOOT TOADS (GENUS *SCAPHIOPUS*)

By HERBERT A. BROWN

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

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THE STATUS OF
CALIFORNIA AND ARIZONA POPULATIONS OF THE WESTERN
SPADEFoot TOADS (GENUS *SCAPHIOPUS*)¹

By HERBERT A. BROWN²

ABSTRACT: Comparisons of morphology and mating calls of *Scaphiopus hammondii* populations from southern California and southeastern Arizona indicate a degree of evolutionary divergence between these geographical isolates that is indicative of reproductive isolation. I propose that the western populations retain the name *Scaphiopus hammondii* (Baird) and that the eastern populations be recognized as *Scaphiopus multiplicatus* (Cope).

An important difference between eastern and western populations is the structure of the male mating call. When mating call characters, normalized to 20°C, are compared, *S. hammondii* calls are short (0.51 sec) and rapidly pulsed (44.5 pulses/sec) while *S. multiplicatus* calls are long (1.12 sec) and slowly pulsed (20.3 pulses/sec.)

A comparison of the reproductive biology of *S. hammondii* and *S. multiplicatus* is presented. Time of reproductive activity, temperature of breeding pools, and thermal tolerances of embryos, larvae and adults indicate that *S. hammondii* are cold-adapted and *S. multiplicatus* are warm-adapted.

INTRODUCTION

Evolutionary relationships of allopatric populations are among the most difficult to determine, and the amphibians provide only a few well studied cases (Blair 1964, 1965; Littlejohn 1969). This study reports on the evolutionary divergence of allopatric populations of the spadefoot toad currently known as *Scaphiopus hammondii*, and it re-examines the systematic status of these two populations.

The geographical and ecological distribution of *S. hammondii* is extensive (Fig. 1), ranging from California to Texas and from Colorado to southern Mexico and occurring in diverse habitats of desert and grassland to chaparral and woodland into pine forest (Zweifel 1956; Lowe 1964). In California *S. hammondii* occurs in the San Joaquin Valley and southern coastal valleys, but it is absent from the arid southeastern regions. In Arizona another population occurs in the eastern and southern portions of the state, but it is absent in the arid western region. The California population is separated from the nearest Arizona population by nearly 300 miles. Thus, California *S. hammondii* constitute an isolate from the more continuously distributed populations occurring through Arizona across New Mexico into Oklahoma, Texas and Mexico.

¹REVIEW COMMITTEE FOR THIS CONTRIBUTION

ROBERT L. BEZY

IAN R. STRAUGHAN

JOHN W. WRIGHT

RICHARD G. ZWEIFEL

²Department of Biology, University of California, Riverside, California 92502. Present address: Department of Biology, Western Washington State College, Bellingham, Washington 98225.

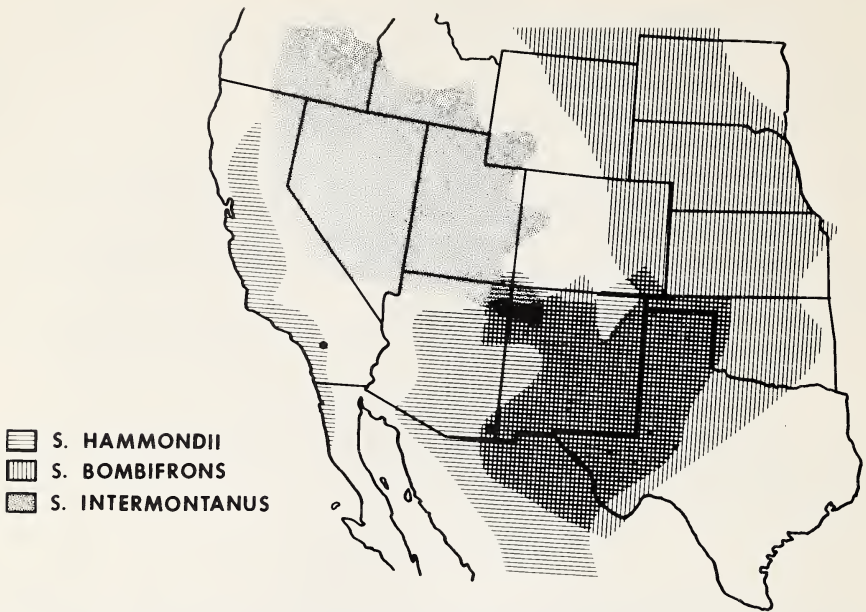


FIGURE 1. Distribution of species of the genus *Scaphiopus*, subgenus *Spea* in the southwestern United States (Stebbins 1966). Collection and study localities in southern California and southeastern Arizona are indicated by solid symbol.

There have already been some comparisons between these populations. Zweifel (1956) found no significant differences in cranial morphology between specimens from California and Mexico. Brown (1967a, 1967b, 1969) studied embryonic and larval adaptations to temperature and found that the summer breeding Arizona populations are warm-adapted and the winter breeding California populations are cold-adapted. The result of artificial hybridization between California and Arizona *S. hammondi* (Brown 1967b) indicated that the populations are genetically compatible since reciprocal crosses produce a high percentage of normal embryonic development; however, the fertility of F_1 hybrids was not determined.

The ranges of *S. hammondi* and *S. bombifrons* (Plains spadefoot toad) overlap in eastern Arizona, New Mexico, western Texas, and northern Mexico (Fig. 1), and this sympatry provides the opportunity of reproductive interactions between these two closely-related species. No such opportunity exists for the California populations of *S. hammondi*. The difference in reproductive environment may influence the evolutionary divergence of two disjunct, allopatric cognate populations (Porter 1968, Littlejohn 1969:462).

The purpose of this study was to evaluate the degree of evolutionary divergence between California and Arizona populations, currently referred to *S. hammondi*, by examining the differentiation of adult morphology and mating call in one population from each of the two areas. This would supplement previous studies and con-

tribute to understanding the development of potential reproductive isolation between California and Arizona populations during geographical isolation. In addition, further information on the reproductive ecology of California *S. hammondi* is presented.

STATUS OF WESTERN SPADEFOOT TOADS

ADULT EXTERNAL MORPHOLOGY

Comparative morphological studies frequently have been used to determine the extent of geographic variation or to evaluate evolutionary divergence between allopatric populations. Firschein (1950) and Zweifel (1956) studied geographic variation in morphology of *S. hammondi*, and both suggested that further study is needed before any taxonomic changes are made. Detailed description of the external features of *S. hammondi* was given by Stebbins (1951:207) and will not be repeated here.

Morphological comparisons were made between one California sample (San Jacinto Valley, near Moreno, Riverside Co., LACM 122867-91) and one Arizona sample (San Simon Valley, near Portal, Cochise Co., LACM 122840-64), each consisting of 25 sexually mature adult males collected during the breeding season. The following measurements were made with vernier calipers and recorded to the nearest 0.1 mm: snout-vent length, head width, interorbital width, tibia-fibula length, height of spade, and width of spade. Measurements of tibia-fibula length were expressed as a ratio of snout-vent length; head length and interorbital width were expressed as a ratio of head width; and the relative size of the spade was expressed by a ratio of spade height to spade width.

A comparison of these measurements (Table 1) suggests that the two populations are similar in most characters, but there are some important differences. The mean

TABLE 1

Morphological characteristics of breeding adult males of *Scaphiopus hammondi* from southern California and southeastern Arizona. Data are mean $\pm$ twice standard error, and range. Sample size = 25 for each population.

	California			Arizona		
Snout-vent length (SV) mm	53.2 $\pm$ 1.38,	45.3 –	58.5	46.9 $\pm$ 1.28	41.0 –	51.9
Tibia length (TL) mm	20.1 $\pm$ 0.38,	18.3 –	22.4	17.8 $\pm$ 0.37,	16.0 –	19.8
Head width (HW) mm	20.6 $\pm$ 0.55,	17.9 –	21.7	17.5 $\pm$ 0.48,	15.2 –	19.1
Head length (HL) mm	11.7 $\pm$ 0.48,	9.9 –	13.9	9.9 $\pm$ 0.25,	8.9 –	10.9
Interorbital width (IW) mm	5.2 $\pm$ 0.26,	3.8 –	6.5	4.4 $\pm$ 0.20,	3.2 –	5.4
Spade height (SH) mm	2.5 $\pm$ 0.24,	2.0 –	3.4	2.6 $\pm$ 0.11,	2.2 –	3.1
Spade width (SW) mm	3.7 $\pm$ 0.16,	2.9 –	4.0	2.8 $\pm$ 0.13,	2.1 –	3.2
100X TL/SV	37.8 $\pm$ 0.3,	34.5 –	40.4	37.9 $\pm$ 0.3,	35.2 –	42.2
100X HL/HW	56.8 $\pm$ 2.0,	45.1 –	65.3	57.1 $\pm$ 1.4,	51.1 –	64.5
100X IW/HW	25.2 $\pm$ 0.5,	21.2 –	29.6	25.1 $\pm$ 0.5,	20.4 –	31.2
100X SH/SW	76.6 $\pm$ 3.6,	60.6 –	103.0	95.5 $\pm$ 3.2,	75.8 –	108.8

snout-vent length of California males is 53.2 mm while that of Arizona males is 46.9 mm; this difference is statistically significant $P < .01$; $t = 6.8$). Chrapliwy (1956: 68) also reported that California specimens (average, 53.3 mm) are larger than those in Arizona, New Mexico, and Texas (average, 47.4 mm). Another important difference (Table 1) is the shape of the metatarsal tubercle (spade). When spade height is expressed as a percentage of spade width, the mean of the California sample (76.6) is significantly less than that of the Arizona sample (95.5) ($P < .01$; $t = 7.9$).

Although there is some overlap in the morphological measurements the two populations are quite distinct in terms of color and color pattern, all individuals being easily allocated on the basis of this one character. In specimens from California, the color and pattern of the dorsum is dark gray-green with distinct, light gray or white, dorsolateral stripes diverging from the head and extending to the sacrum; the pigmentation of the eye (iris) is conspicuously variegated with bright yellow and black. This description is the same as the illustration of *S. hammondii* (from central California) presented by Stebbins (1966: plate 8). In specimens from Arizona the color of the dorsum is uniformly brown or dark tan, and dorsolateral stripes are usually not evident; the iris is slightly variegated and appears pale copper.

MATING CALL COMPARISONS

Recordings of mating calls of individuals at natural breeding sites were made with a battery-operated tape recorder (Stancil-Hoffman) at a tape speed of $7\frac{1}{2}$ inches per second and an Altec microphone (633A). At least six calls per individual were recorded. Water and air temperature were taken at one inch below the water surface and one inch above, respectively, using a Schultheis rapid reading thermometer. Analysis of the mating calls was made by using a "Sonagraph" (Kay Electric Co.) that produces a sound spectrogram with a frequency range to 8,000 cycles per second over a time period of 2.4 seconds. Four variables of the mating call were obtained from the spectrogram: duration of call in seconds, pulses per call, rate of pulse production in pulses per second, and dominant frequency. The tape-recordings have been deposited at the Natural History Museum of Los Angeles County.

In addition to recording mating calls of *S. hammondii* in California and Arizona, mating calls of *S. bombifrons* and apparent hybrids between *S. hammondii* and *S. bombifrons* were also recorded in the San Simon Valley of southeastern Arizona. The structure of the mating calls of *S. hammondii* and *S. bombifrons* have been described for sympatric populations in western Texas (Blair 1955; Forester 1973) and southwestern New Mexico (Bogert 1960; Pierce 1976); apparent hybrids between *S. hammondii* and *S. bombifrons* were also recorded in southwestern New Mexico by Bogert (1960). There are no published accounts of the mating call of California *S. hammondii*.

I made tape-recordings of *S. hammondii* in California on three occasions at two localities in the San Jacinto Valley (Riverside Co.): (1) four males were recorded on 30 March 1965 in shallow pools along the San Jacinto River about two miles north of Lakeview when the water temperature was 12°C and the air temperature was 9°C ; (2) three males were recorded on 24 March 1966 in deep pools of a gravel

pit about three miles east of Moreno when the water temperature was 13.4°C and the air temperature was 8°C; (3) two males were recorded on 26 March 1966 at the gravel pit just described when the water temperature was 19°C and the air temperature was 13.8°C.

In southeastern Arizona and southwestern New Mexico tape recordings of *S. hammondi*, *S. bombifrons*, and apparent hybrids (*S. hammondi* X *S. bombifrons*) were made during July 1965 near the following localities: Portal and Wilcox (Cochise Co.) Arizona; Rodeo, Animas, and Lordsburg (Hidalgo Co.), New Mexico. Water and air temperatures at the time of these recordings were 18-24°C and 22-26°C, respectively.

The basic call structure of *S. hammondi* recorded in California and Arizona resembles the pattern described by Blair (1955): the call is distinctly trilled. Representative sonagrams of the calls of these two populations are presented in Fig. 2, and the physical characteristics are given in Table 2. Before comparisons were made, however, calls were adjusted for temperature. Previous studies have demonstrated that call length varies inversely with temperature while pulse rate varies directly (see Zweifel 1968a; Forester 1973). Arizona mating calls were recorded when water temperature was about 20°C, but California calls were recorded at 12, 13.4, and 19°C (Table 2). I analyzed the California data and calculated the following regression-

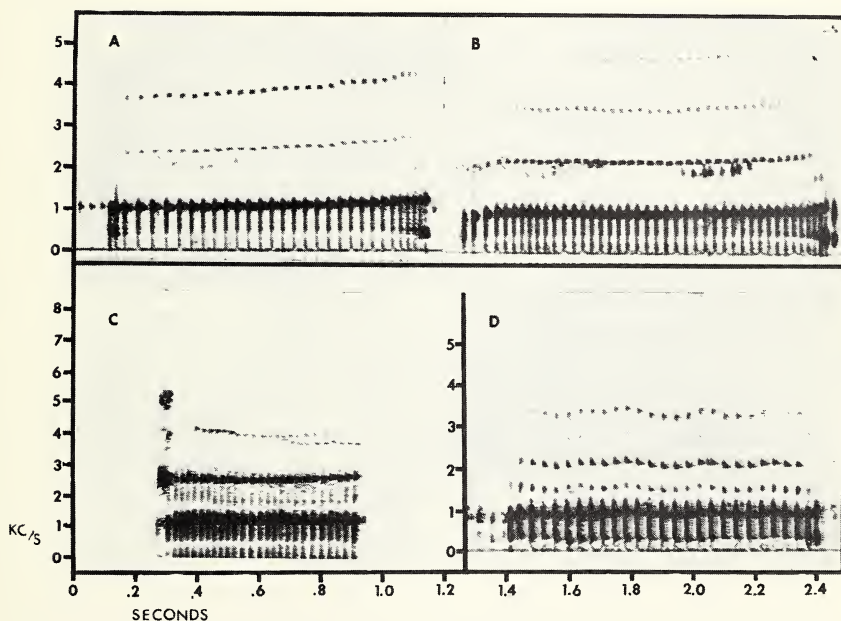


FIGURE 2. Sound spectrograms of *Scaphiopus hammondi* mating calls. California call recorded at 12°C (A), at 13.4°C (B), and at 19°C (C). Arizona call recorded at 20°C (D).

TABLE 2

Mating call characteristics of *Scaphiopus hammondi* from California and Arizona.
Data are mean and range

Number of Individuals	Temperature °C	Call Length (seconds)	Pulses per Call	Pulses per Second	Dominant Frequency (cycles per second)
California					
4	12	1.05 (0.86-1.18)	35.7 (27-45)	33.8 (29.5-37.2)	1450-1550
3	13.4	1.17 (1.05-1.25)	34.8 (32-38)	29.4 (27.8-31.5)	1370-1550
2	19	0.57 (0.50-0.65)	24.3 (22-26)	43.1 (39.7-47.2)	1490-1600
	20 ^a	0.51 (0.32-0.64)	22.7 (16.7-28.9)	44.5 (39.7-50.2)	
Arizona					
8	20	1.12 (1.05-1.25)	25.0 (21-28)	21.3 (20.2-24.5)	1400-1550

^aData adjusted to 20°C.

equations describing the influence of temperature on characteristics of the mating call: (1) call length on temperature, $Y = 2.1 - 0.08X$; (2) pulses per call on temperature, $Y = 56.8 - 1.7X$; (3) pulse rate on temperature, $Y = 10.8 + 1.7X$. The data of the California calls adjusted to 20°C are also given in Table 2. When compared at 20°C the mean call length for the California sample (0.51 sec) is significantly shorter than the Arizona sample (1.12 sec); values of mean pulses per call are similar (22.7 and 25 pulses per call), but mean pulse rate of the California sample (44.5/sec) is twice that of the Arizona sample (21.3/sec). In summary, California calls are short and rapidly pulsed but Arizona calls are long and slowly pulsed.

There is additional information on the structure of the mating call of *S. hammondi* from other regions (central California, Arizona, New Mexico and western Texas). These data are summarized in Table 3. The mating calls recorded by Stebbins near O'Neals in central California (about 260 miles north of my study in the San Jacinto Valley) are shorter in call length (0.7 and 0.8 sec), but length of call is often variable and may reflect the degree of sexual excitement of the calling male (Porter 1964, Zweifel 1968a); in comparing pulse rates, however, the central California calls (30 and 32/sec) are similar to those from southern California (33.8/sec).

Tape-recordings of *S. hammondi* from Arizona at Avra Valley and Sierra Vista were provided by W. F. Blair (Univ. of Texas, Austin), and I made sonagrams of some of these calls for comparison with my recordings. The sample from Avra Valley (160 miles west of the San Simon Valley site of my study) was recorded at a water temperature of 28°C. Considering this high temperature and the positive influence of

TABLE 3

Mating call characteristics (call length and pulse rate) of *Scaphiopus hammondi* from other localities in California, Arizona, New Mexico, and Texas

Locality	Call			Source
	Temp °C	Length (sec)	Pulse Rate (pulses/sec)	
California				
San Joaquin Experimental	12.8	0.70	30	R. C. Stebbins, (Mus. of Vert. Zool., Berkeley, California)
Station, O'Neals (Madera Co.)	12.8	0.80	32	
Arizona				
Avra Valley, West of Marana	28	0.70	30.5	W. F. Blair (Univ. of Texas, Austin)
(Pinal Co.)				
Sierra Vista (Cochise Co.)	19.5	1.20	22	
New Mexico				
Rodeo (Hidalgo Co.)	20	0.97	26	Bogert (1960)
Texas				
Valentine (Jeff Davis Co.)	23	0.95	20.1	Blair (1955)
Tulia (Swisher Co.)	18	1.09	18.4	Blair (1955)
Lubbock (Lubbock Co.)	20	0.95	22.5	Forester (1973)

increasing temperature on pulse rate, the value of pulse rate in this sample (30.5/sec) is higher than my Arizona sample (21.3/sec) but still lower than the California sample (43.1/sec) recorded almost ten degrees lower (19°C). The mating calls from the Sierra Vista locality (about 80 miles west of the San Simon Valley) are similar to those in southeastern Arizona.

Mating calls of *S. hammondi* recorded in New Mexico by Bogert (1960) and in Texas by Blair (1955) and Forester (1973) are similar to those of the San Simon Valley of southeastern Arizona.

Forester (1973) also studied the effect of temperature on call length and pulse rate of mating calls of *S. hammondi* from northwestern Texas. When his data are adjusted to 12°C for comparison to my data on California calls, the value of call length is 1.01 seconds and pulse rate is 18.3/second; in the California sample call length is 1.05 seconds and pulse rate is 33.8/second. In Forester's study the pulse rate increased 0.5 pulses per second per degree centigrade increase but my data on California calls indicate that this increase is 1.7 pulses per second per degree centigrade increase. Thus, pulse rate in California calls is more sensitive to temperature change than that of northwestern Texas calls.

The mating call of *S. hammondi* in Mexico is poorly known, but Bogert (1960: 285) reported that "there are few important differences between calls of a population at Chapala, Jalisco, Mexico . . . and those of populations in Arizona . . ."

The reproductive environment of *S. hammondii* in southeastern Arizona differs from the population in California in that *S. bombifrons* in the San Simon Valley breed in the same temporary pools as *S. hammondii*. This sympatric distribution extends across New Mexico into western Texas. A limited amount of hybridization occurs between *S. hammondii* and *S. bombifrons* in southeastern Arizona (Bogert 1960), southern New Mexico (Creusere and Whitford 1976), and western Texas (Forester 1973); this is indicated by the incidence of interspecific amplexus and the presence of calling male hybrids in the breeding pools.

On the basis of mating call analysis two distinct call types of *S. bombifrons* are recognized (Pierce 1976): fast trill and slow trill. Table 4 compares the mating calls of two populations of *S. hammondii* sympatric with *S. bombifrons* and the disjunct, allopatric population of *S. hammondii* from California. In southeastern Arizona *S. bombifrons* represents a fast call type, and in western Texas the populations represent the slow call type. There are no differences in call structure between Arizona and Texas populations of *S. hammondii*. However, the California population of *S. hammondii* has a call pattern different from that of *S. hammondii* in Arizona and Texas. The California calls are more similar to those of *S. bombifrons* of western Texas. Porter (1964) suggested that "... in completely allopatric situations, in which no selection for call differentiation would be present, relatively distantly related species might possess similar calls, like that of their common ancestor." The similarity in mating call between the fast trill (California) *S. hammondii* and the slow trill (eastern) *S. bombifrons* suggests that these populations may have retrained the ancestral, or primitive, mating call pattern for the two species. The very different mating calls in southwestern New Mexico and southeastern Arizona could be considered the result of more recent evolution and be described as advanced.

The call differences in sympatric populations of *S. hammondii* and *S. bombifrons* apparently function as effective premating isolation mechanisms. Forester (1973)

TABLE 4

Comparisons of call length and pulse rate in *Scaphiopus hammondii* and *Scaphiopus bombifrons*. All data (mean and range) adjusted to 20°C

Population	Call Length (seconds)	Pulse Rate (pulses/second)	Source
southern California			
<i>S. hammondii</i>	0.51 (0.32-0.64)	44.5 (39.7-50.2)	Present study
southeastern Arizona			
<i>S. hammondii</i>	1.10 (1.00-1.20)	22.3 (19.2-24.3)	Present study
<i>S. bombifrons</i>	0.12	250.0	Bogert (1960)
western Texas			
<i>S. hammondii</i>	0.95 (0.77-1.21)	22.5 (18-25)	Forester (1973)
<i>S. bombifrons</i>	0.53 (0.39-0.72)	63.0 (54-75)	Forester (1973)

reported that in northwestern Texas females of both species can respond to the homo-specific male mating calls and that females can also discriminate between homospecific and heterospecific male mating calls. In southwestern New Mexico and southeastern Arizona where the call differences appear the greatest, hybridization is infrequent. Apparent male hybrids can be recognized by their distinctive mating call (Table 5 and Fig. 3); the call is short (0.39 sec) with a high pulse rate (50.7/sec) but the trills are discernible. These data support the values reported by Bogert (1960:285) where call length is 0.42 seconds and pulse rate (calculated from his data) is 52/second. Jack R. Pierce reported (see Wasserman 1970: 244) that male hybrids (recognized by their mating calls) are sterile in backcrosses to parental forms (in southwestern New Mexico). Forester (1975) reported, however, that male hybrids from northwestern Texas are fertile in backcrosses. The difference in fertility of hybrids would be explained by accepting the suggestion that the southwestern New Mexico populations of *S. bombifrons* are really a third undescribed species (see Pierce 1976).

CALLING POSITION AT BREEDING POOL

While sympatric populations of *S. hammondi* and *S. bombifrons* may breed in the same temporary pool, there are distinct differences in the position of males calling at the breeding pool. Males of *S. hammondi* call while floating and swimming at some distance from the pool's edge, but males of *S. bombifrons* call at the edge of the pool while sitting in shallow water (Lowe 1954, Gehlbach 1956, McAlister 1959). I observed these different behaviors in the San Simon Valley of southeastern Arizona. In California, however, males of *S. hammondi* have a preference to call from a concealed position near the edge of the pool; on several occasions males were found sitting and calling at the edge of the pool with only a part of their body immersed. Calling males were seldom observed in an open area of the pool. Gehlbach (1965) reported that in northwestern New Mexico, where *S. hammondi*, *S. bombifrons* and *S. intermontanus* occur together, *S. hammondi* males may call from shallow water or from shore; no *S. bombifrons* were found calling at this site even though they were present in this region. These field observations indicate that males of *S. hammondi* may prefer a more peripheral calling position when other closely-related spadefoot toads are not present in the breeding chorus.

TABLE 5

Mating call characteristics of three apparent hybrids, *Scaphiopus hammondi* X *S. bombifrons*, recorded near Rodeo, New Mexico

Individual	Water Temperature °C	Call Length (seconds)	Pulses per Call	Pulses per Second
1	17.8	0.36-0.41	19-21	50.0-52.8
2	19.6	0.36-0.40	18-20	50.0-52.6
3	18.4	0.38-0.40	19-21	50.0-52.5

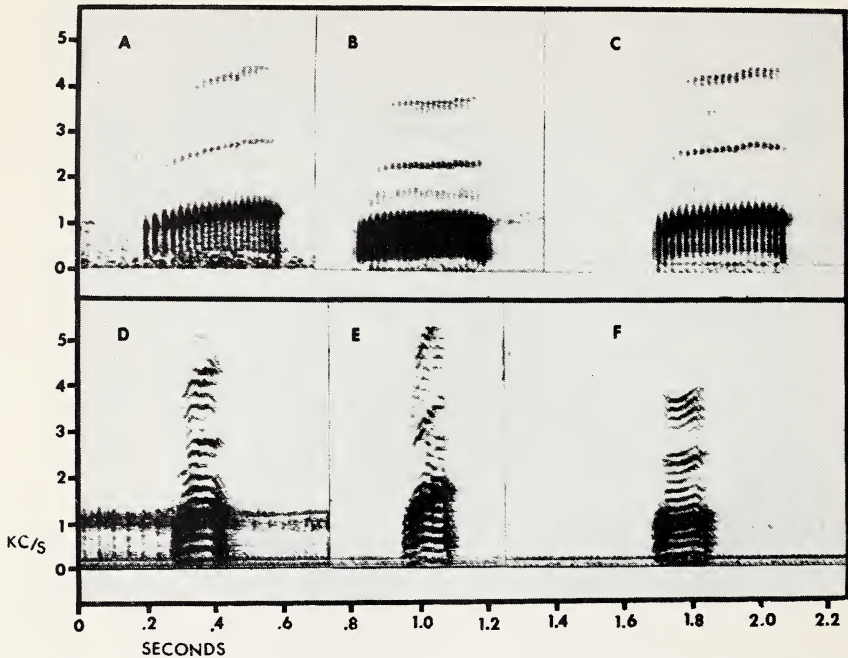


FIGURE 3. Sound spectrograms of mating calls of three apparent hybrids, *Scaphiopus hammondi* X *Scaphiopus bombifrons* (A, B, C) and three *Scaphiopus bombifrons* (D, E, F) recorded near Rodeo, New Mexico at a water temperature of 18.4°C.

REPRODUCTIVE ECOLOGY OF *SCAPHIOPUS HAMMONDII* IN CALIFORNIA

Field observations on the breeding activity of *S. hammondi* in the San Jacinto Valley suggest that reproduction only occurs in late winter and spring. During the fall and winter from October to December the adults and immature toads may emerge after periods of wet weather, but no reproduction occurs at this time. The period of June through September corresponds to the hot, dry season and the toads are usually inactive and assumed to be beneath the soil.

Reproduction of spadefoot populations in the San Jacinto Valley was observed during four years (1963 to 1967), but the years 1964 to 1966 were studied more intensively. During November and December of 1964 a total of 2.36 inches of rain fell in the San Jacinto Valley and toads emerged, but they did not breed. Then a warm, dry period (January and February 1965) followed and the pools formed by the earlier winter rainfall became dry. During March and April of 1965 storms deposited 6 inches of rain and toads began chorusing in the refilled breeding pools. Calling males were heard from March 13 to April 23 when water temperatures ranged from 6° to 15°C. Gravid females were found near the breeding pools on March 15, 17, and 31. Intermittent rain was common between March 13 and April 11, but following this period no measurable rain was recorded in the San Jacinto Valley. Despite the absence of rain the toads continued to chorus in the temporary pools.

On 28 April 1965 I found spadefoot tadpoles in the temporary pools along the San Jacinto River near Lakeview; the tadpoles had developed to stages 30-34 of Gosner (1960) with well developed hindlimbs. On May 1 at the pools near Moreno I found tadpoles in stages 28-41. By May 10 the Lakeview tadpoles were at stages 40 and 42, some with front legs protruding. On May 30 the Lakeview pools contained many tadpoles with all four legs but still with long tails; in addition many recently transformed juveniles were hiding in the deep mud cracks of the drying pools. The average snout-vent length in a sample of twenty juveniles was 28 mm (range, 23-33). Oviposition probably began about March 13, and presumably took place several times later because metamorphosing tadpoles were found from May 10 to May 30. The period from oviposition to metamorphosis was about 55-60 days.

Further observations on the breeding activity of the San Jacinto Valley populations were made during the 1965-1966 season. In the fall and winter of 1965 from November 14 to December 31 the San Jacinto Valley received considerable rainfall (10.2 inches), and the usual breeding pools formed. Despite the abundant rainfall, available breeding pools, and moderate water temperatures (11 to 15°C) the spadefoot toads did not breed. Adult and immature toads were found on the wet roads and near the breeding pools, but I found only one small chorus on November 22. On subsequent visits (December and January) to this site no tadpoles were found in the pools.

During the following three months only 2.2 inches of rainfall was recorded in the San Jacinto Valley: January, 0.71; February, 1.01; March, 0.47. On February 5, I found a gravid female and a small group of calling male toads at the breeding pools near Moreno. On February 8 chorusing activity continued at the Moreno pools. On March 24 a convectional storm produced a series of light showers in the San Jacinto Valley, and a large group of about thirty calling toads were observed at the Moreno pools; water temperatures ranged from 13° to 19°C for the next several days, and toads continued to chorus at this site until April 14. However, no rainfall was recorded at this site after the light showers of March 24. The pattern of continued chorusing activity in the absence of rainfall is similar to spadefoot behavior observed the previous year. Storer (1925:156) reported similar observations on populations of *S. hammondi* near Banning (Riverside Co.), California. Zweifel (1956:42) reported that *Scaphiopus intermontanus* may chorus in the absence of rain also.

The following summary of terrestrial and reproductive activity of California populations of *S. hammondi* is based upon personal field observations and examination of museum specimens and field notes of the following institutions: Museum of Vertebrate Zoology (Berkeley); California Academy of Sciences (San Francisco); and the former collection of the Stanford Natural History Museum (Palo Alto) now transferred to the California Academy of Sciences. Spadefoot toads have been collected in every month of the year except August. While chorusing activity may occur from November to July, eggs have been found only during February, March and April, and tadpoles during January to June. Metamorphosing tadpoles have been found from March through June. These observations suggest that the usual period of reproduction is January to April.

The breeding season of California *S. hammondi* occurs during the months of high and frequent rainfall and low temperatures. In the San Jacinto Valley most rainfall

occurs from December to March with the maximum during February. The period when rainfall is frequent is January to April when there are six rainy days per month (U.S. Weather Bureau records). In contrast, Arizona populations of *S. hammondi* breed following the heavy rain and high temperatures of the summer months of July and August (Brown 1967b). Thus, California populations of *S. hammondi* are cold weather breeding, while Arizona populations are warm weather breeding or they breed when it rains at temperatures above 10°C.

In previous studies (Brown 1967a, 1967b) I compared the embryonic temperature adaptations of California and Arizona *S. hammondi* and found that California embryos have lower limits of tolerance (9° and 30°C) than Arizona embryos (13° and 32.5°C), and that California embryos have rapid developmental rates at low temperatures. Although I did not find eggs in the natural pools in California, Robert C. Stebbins (field notes) found embryos exposed to water temperatures of 7.7° to 15.6°C in the morning, 19.9°C in the afternoon, and 11.3°C in the evening at the San Joaquin Experimental Station on 11-13 March 1951; eggs deposited on the evening of March 10 hatched by the morning of March 13. I also studied the temperature adaptations of control and hybrid tadpoles made from crosses between California and Arizona *S. hammondi* (Brown 1969). These data suggest that Arizona tadpoles are more resistant to high temperatures than California tadpoles. Brattstrom (1968:103, Fig. 3h) reported that the critical thermal maximum of adult *S. hammondi* is higher for individuals from Sonora, Mexico than those from southern California. These data indicate that California *S. hammondi* have a cold-adapted physiology allowing them to take advantage of the winter and spring rainfall.

Another spadefoot toad, *Scaphiopus couchi*, occurs in California but it is restricted in distribution to the extremely arid, southeastern part of the state (Mayhew 1962). Although most rainfall comes to this region during the winter months, *S. couchi* does not respond to this rainfall but breeds only following the very infrequent heavy rains of the summer months (Mayhew 1965). While *S. hammondi* in California is a cold-adapted toad, *S. couchi* is an apparently warm-adapted toad that breeds in warm weather and has high embryonic thermal limits (15.5° and 34°C) and the most rapid rate of development of any North American anuran (Zweifel 1968b).

EVOLUTIONARY DIVERGENCE AND TAXONOMY

This study of allopatric populations of *S. hammondi* indicates considerable evolutionary divergence in morphology, breeding habits, mating calls, and physiological temperature adaptations (Table 6). The populations have presumably been separated at least since some time in the Pleistocene (Brown 1967b). The differences are presumedly adaptive and attributable to selection in different climatic and biotic environments. The color differences may represent matching of different backgrounds and the shape of the metatarsal tubercle may relate to differences in the physical characteristics of the soil where the toads burrow (Wasserman 1957). Divergence in temperature tolerances is consistent with the rainfall patterns in the two areas. While the differences in mating calls and breeding behavior may be important potential pre-

TABLE 6

Summary of the characteristics of two species of western spadefoot toads, *Scaphiopus hammondi* and *Scaphiopus multiplicatus*

Character	<i>S. hammondi</i> (California)	<i>S. multiplicatus</i> (Arizona)
1. Morphology		
Coloration of body	Green	Brown
Coloration of eye	Yellow and black variegation	Copper
Body length of adult males	53.2 mm	46.9 mm
Shape of spade (SH/SW)	0.77	0.96
2. Reproductive Biology		
Breeding season	January-April	July and August
Embryonic temperature tolerance	9-30°C	13-32.5°C
Developmental rate (hr, 28°C)	25.1	21.7
Tadpole temperature tolerance	Hybrid > Control	Control > Hybrid
3. Genetic Compatibility		
Intraspecific crosses ^a	CH × AH, normal	AH × CH, normal
Interspecific crosses ^a	CH × AB, normal	AH × AB, normal
	CH × I, normal	AH × I, normal
Fertility of hybrids	Not known	Male hybrids (AH × AB) may be sterile.
4. Breeding Behavior		
Mating call duration at 20°C	0.51 seconds	1.12 seconds
Mating call pulse rate at 20°C	44.5/second	21.3/second
Calling position of male at breeding pool	Swimming-floating near shore	Swimming-floating away from shore

^aCH = California *S. hammondi*; AH = Arizona *S. multiplicatus*; AB = Arizona *S. bombifrons*; I = *S. intermontanus* from eastern California.

mating isolation mechanisms, the two populations are interfertile and have no apparent postmating isolation mechanisms. This pattern of evolutionary divergence follows that described by Blair (1964) where differentiation of the mating call and development of ecological isolation mechanisms have preceded the development of genetic incompatibility.

The taxonomic status of the North American pelobatine toads, *Scaphiopus* (Holbrook) and *Spea* (Cope), and their phylogenetic relationships have been reviewed by Zweifel (1956), Kluge (1966) and Estes (1970). These studies recognize three species of the subgenus *Spea*, *Scaphiopus hammondi*, *Scaphiopus bombifrons* and *Scaphiopus intermontanus*. It is my opinion, after studying male mating calls, adult morphology, breeding behavior, and physiological temperature adaptations (Table 6), that the biological differences found between western and eastern populations of *S. hammondi*, are the same order of magnitude as that observed between related

sympatric species. I therefore suggest that the western population retain the name *Scaphiopus hammondi* (Baird) and that the eastern population be recognized as *Scaphiopus multiplicatus* (Cope).

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This report is dedicated to the memory of my son Steven who died of leukemia at age 5 on 11 December 1975. Steven was a happy, loving boy who helped make life more cheerful for all his many friends.

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